Plastic pioneers: Hominin biogeography east of the Movius Line during the Pleistocene

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ABSTRACT

While the "Movius Line" may no longer represent a valid cultural division between Early and Middle Pleistocene hominins in South and Southeast Asia, it still offers a useful geographical and ecological window into changing processes of colonization by different members of the genus *Homo*. In this paper, we initially review the palaeoenvironmental and cultural record associated with *Homo erectus* and *Homo floresiensis* to argue for a relatively homogeneous adaptive strategy utilized by hominins moving east of this notional line during the Early and Middle Pleistocene. We then contrast this to the rapid dispersal of *Homo sapiens* into South Asia, Southeast Asia, and Melanesia, from at least 45,000 years ago, associated with specialized subsistence and technological adaptations to a variety of environmental settings. While earlier members of our genus appear to have followed riverine and lacustrine corridors, whose situation varied with periods of climate change, *Homo sapiens* specialized in adaptations to tropical rainforests, faunally depauperate island settings, montane environments, and deep-water marine habitats. After evaluating whether this distinction may be one of taphonomic and survey bias, and reviewing potential methodological developments that may facilitate further investigation, we suggest that the adaptive and cultural plasticity of our species enabled pioneering colonization and occupation not previously seen in this part of the world. This plasticity allowed our species to remain in this region through ever-increasing climatic instability and become the last surviving hominin in Late Pleistocene South Asia and Sahul.

1. Introduction

The capacity of our species, and its hominin ancestors, to spread beyond the African evolutionary cradle and into Eurasia has remained a key focal point of research in palaeoanthropology and archaeology (Dennell and Roebroeks, 2005; Rabett, 2012; Dennell, 2016). In the 1940s, Hallam Movius (1944, 1948) drew a line that separated the Early Palaeolithic world of Eurasia into a region defined by Acheulean bifaces in Africa, western Europe, Southwest and South Asia, and a region characterized by unstandardized cores and flakes in East and Southeast Asia (Dennell, 2016). Movius argued that these different industries were produced by hominins of 'different branch[es] of the human stock' (1948: 408), and that technological patterning was a result of behavioural and biological differentiation. Although the relevance and utility of this line as a meaningful technological and cultural boundary has now been heavily disputed (Lycett and Bae, 2010; Dennell, 2014, 2016), the tropical environments of Southeast Asia, and also Melanesia, on the east of Movius' division have continued to be considered a significant 'barrier' to the expansion of Pleistocene hominins. For example, it has been argued that Early and Middle

Pleistocene hominin expansions into Southeast Asia and Melanesia were only possible with the development of savanna corridors during dry climatic phases (Gamble 1993; Dennell and Roebroeks, 2005). Such corridors were also thought to be crucial to the movement of our own species into the region until relatively recently (Gamble 1993; Bird et al., 2005; Boivin et al., 2013).

The current state of knowledge in terms of the fossil and lithic record of Early-Late Pleistocene East and Southeast Asia has been excellently reviewed elsewhere (e.g. Dennell et al., 2014; Kaifu et al., 2015; Kaifu, 2017; Bae et al., 2017). In traditional discussions, the main candidate for early hominin movements east of the Movius line has been *Homo erectus* populations, ultimately originating in Africa. Nevertheless, as summarized by Kaifu (2017), there remains debate as to whether *Homo floresiensis* may possibly represent a separate Pliocene lineage that also moved across Asia during the Pleistocene, as well as to whether complex population admixture and regional development also played a major evolutionary role. For example, Kaifu (2017) notes clear morphometric distinctions between fossils identified as 'H. erectus' in Java, northern China, southern China, 'late archaic' populations found in China, and the Maba and Narmada fossils of southern China and

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India, respectively. Certainly, much remains to be discovered in terms of population relationships and variability across Early and Middle Pleistocene East and Southeast Asia, however additional review is beyond the scope of this paper. Instead, we focus primarily on mainland and island Southeast Asia and Sahul as a region with broadly agreed upon fossil affinities. In each case, we refer to the fossil identification provided by the authors of the cited papers, noting taxonomic debate throughout where it is found. Given the palaeoanthropological, archaeological, and palaeoecological analyses continuing across East Asia, we hope a similar review will be possible for that region in due course.

With this in mind, in this paper we review the ways in which the Movius Line, or at least the relevant regions involved in the definition of this Line, has morphed from a technological and cultural division into a biogeographical boundary of hominin expansion from the Early to the Late Pleistocene. Given our primary focus on Southeast Asia and Melanesia this involves the consideration as to whether different tropical forest formations were hospitable to hominins moving from more temperate or arid biomes to the north and west. Tropical forests, and tropical rainforests in particular, have been considered to provide a dearth of protein and carbohydrate resources, to represent dangers in terms of disease and poisonous animals and plants, and to hinder effective hominin thermoregulation (Hart and Hart, 1986; Bailey et al., 1989; Bird et al., 2005). In Southeast Asia and Melanesia a huge variety of tropical forest formations, ranging from seasonally cold montane rainforest, starch poor peat swamp forests, and faunally depauperate island tropical forests add to these adaptive challenges (Roberts and Petraglia, 2015; Summerhayes et al., 2017; Roberts and Stewart, 2018). Here, we compare the current evidence for Early and Middle Pleistocene hominin adaptations to Southeast Asian environments with those documented for our own species in Southeast Asia and Melanesia during the Late Pleistocene. We evaluate to what extent the regional and environmental focus of the Movius Line remains useful in discussions of hominin biogeography and behaviour.

2. Drawing the line? – Technological and ecological bases of the Movius Line

The Movius Line is a bi-product of one of the major problems with forming detailed narratives in palaeoanthropology, the lack of hominin fossils. This is particularly the case outside the East African Rift and further back in time beyond the Late Pleistocene. As a result, stone tools have often formed a central focus for those seeking to understand the cultural and cognitive capacities of our hominin ancestors. The Acheulean has been especially prominent in this regard, with its bifacially produced handaxes being associated with the emergence of the specialist biped hominin, *H. erectus* and, perhaps later, *Homo heidelbergenesis* (Asfaw et al., 1992; Clark, 1994). The production of these bifacial handaxes during the Early and Middle Pleistocene has been linked to a considerable development in cognitive planning and capacity amongst *H. erectus* (Gowlett, 1984; Wynn, 1991). Yet, despite the arrival of this hominin on Java in tropical Southeast Asia by 1.5 Ma (Zaim et al., 2011), the Acheulean has been considered absent from this region. Indeed, it has been considered largely lacking to the north and east of India and Bangladesh more broadly in Eurasia (Ambrose, 2001). Instead, core and flake industries are prominent in East and Southeast Asia (Lycett and Bae, 2010), leading Movius to suggest the hominins beyond this boundary were culturally or biologically hindered. It has also been argued that this line is linked to a lack of suitable fine-grained raw materials (Movius, 1948; Schick and Zhuan, 1993; Bar-Yosef et al., 2012).

Discoveries of bifacially-flaked material from China and Korea have led to calls for the complete overhaul of the 'Movius Line' as a theoretical entity, however (Dennell, 2014, 2016; Li et al., 2014, 2016). Moreover, generalizations of raw material availability across a large region have been recognized as insufficient (Schick, 1994). In addition,

handaxes from Sangiran on Java, Liang Bua and Wolo Sege on Flores, and the Philippines, have been reported, though little information on them has been published besides the fact that they bear a resemblance to Indian handaxes (Pawlik, 2004; Mishra et al., 2010; Lycett and Bae, 2010; Brumm et al., 2010; Brumm and Moore, 2012; Patole-Edoumba et al., 2012). While some have focused on the bifacial tools of the Chinese Lower Palaeolithic as independent traditions that developed *c.* 1 Ma (Corvinus, 2004; Petraglia and Shipton, 2008; Wang et al., 2012), and others have suggested East and Southeast Asian bifaces have considerable differences to those found in African and western Eurasia (Norton et al., 2006; Norton and Bae, 2008), the fact that bifacial tools are found alongside non-bifacial tools in this region, notably at sites within the Bose Basin, Luonan Basin, and Danjiankou Reservoir Region within China (Lycett and Bae, 2010), seemingly refute the 'Movius Line' as a meaningful cultural or cognitive boundary. Indeed, systematic morphological comparisons of East Asian, African, and western Acheulean assemblages suggest that bifacial differences are quantitative (both in terms of frequency and thickness differences) rather than qualitative (Norton et al., 2006; Petraglia and Shipton, 2008).

Intensifying research into the Late Pleistocene of East and Southeast Asia has also begun to change perceptions of 'core and flake' industries. For example, the Hoabinhian toolkits of simple, flaked cobble artefacts, traditionally dated to the Terminal Pleistocene in Vietnam (Kipfer, 2000; Bellwood, 2007; Matsumura et al., 2015), are very different to the microliths of the Magdalenian and Mesolithic, as well as the Later Stone Age of Africa (Ambrose, 2002), that appear west of the Movius Line at this time. Nevertheless, these technologies are found with bone tools (Matthews, 1966) and complex foraging strategies including the procurement of shellfish, fish, plants, and mammals (Gorman, 1970, 1971), suggesting that it is dangerous to assume 'core and flake' industries are synonymous with cultural or cognitive limitation. Gorman (1970) even argued that Hoabhinian-using communities at Spirit Cave in Thailand were foraging, and perhaps also managing, diverse tropical plants including *Prunus* (almond), *Terminalia*, *Areca* (betel), *Vicia* (broadbean) or *Phaseolus*, *Pisum* (pea) or *Raphia Lagenaria* (bottle gourd), *Trapa* (Chinese water chestnut), *Piper* (pepper), *Madhuca* (butternut), and *Canarium* for food and medicinal uses. At the very least, the extension of the Hoabhinian back to 43.5 ka (Ji et al., 2016), and across Island and Mainland Southeast Asia, as well as China (Ji et al., 2016), suggests that unilinear treatment of Pleistocene 'core and flake' industries is problematic.

Moving past its validity as a technological, cultural, or cognitive boundary, researchers have also tried to formulate the 'Movius Line' as a behavioural point of interest in other respects. For example, Lycett and Bae (2010) have suggested that it represents a demographic boundary between larger, closer populations with effective cultural transmission to the west, and smaller, more diffuse communities to the north and east (Lycett and Bae, 2010). A more popular formulation in recent times has been the 'Bamboo Hypothesis' that suggests that hominins to the north and east of the Movius Line used plants, rather than lithics, to make cutting tools (Brumm, 2010). Experimental and use-wear work has shown how core and flake assemblages can efficiently turn plants, such as bamboo, into effective tools, with characteristic use-wear left on the lithic technology from this practice (West and Louys, 2007; Bar-Yosef et al., 2012; Xhauflair et al., 2016). This has yet to be directly observed on Pleistocene lithic assemblages, and it is unlikely that the bamboo or plant tools themselves will ever be preserved in archaeological sites, particularly in the tropics. Nevertheless, although researchers have noted that bamboo itself is highly sensitive to environmental changes, and likely fluctuated throughout the Pleistocene of East and Southeast Asia (Brumm, 2010; Lycett and Bae, 2010; Bar-Yosef et al., 2012), variability in technological assemblages identified by the Movius Line is likely to be better explained by local adaptations, rather than generalized cognition or culture (see also Petraglia and Shipton, 2008).

Irrespective of technological remnants it is clear that Early/Middle

Pleistocene *Homo,* as well as our own species in the Late Pleistocene, was able to get beyond the Movius Line and even beyond the formal, biogeographical Wallace Line. This is potentially adaptively significant because modern biogeographic divisions (Holt et al., 2012) map onto the regional division brought into focus by the Movius Line. In particular, Southeast Asia represents the largest tropical rainforest block to be encountered by hominins following their expansion beyond Africa (Whitmore, 1998; Ghazoul and Sheil, 2010), while Island Southeast Asia and Oceania also include insular settings that necessitate ocean crossings and adaptations to depauperate fauna (Samper Carro et al., 2016). Given theoretical debate regarding the attractiveness of these habitats to hominin occupation (Bailey et al., 1989; Gamble 1993; O'Connor et al., 2011; Roberts and Petraglia, 2015; Samper Carro et al., 2016), as well as potential fluctuations in the extent of these environments in the past, the Movius Line may represent a useful regional device for comparing the adaptive capacities of Early/Middle Pleistocene *Homo* taxa (namely *H. erectus* and *H. floresiensis*) to those of our own species, *Homo sapiens*. Moving beyond a technological, cultural, or cognitive definition, we seek to evaluate whether the Movius Line represents a useful theoretical focus when reviewing current climatic, environmental, and ecological data associated with Pleistocene hominins in Southeast Asia and Melanesia.

3. Southeast Asian (and Oceanian) biogeography

On the basis of older and more recent zoogeographic analyses, Mainland and Island Southeast Asia lie within the 'Oriental' biogeographic sphere (Watts, 1984; Holt et al., 2012), separate to the 'Palearctic' and 'Sino-Japanese' regions to the north, and the 'Saharo-Arabian' and 'Afrotropical' regions to the west. Within the Oriental region an important subdivision exists between the more seasonal and more arid Indochinese province, that includes northern Thailand, South China, Myanmar, Vietnam, Laos, and Cambodia, and the wetter, less seasonal Sundaic province that incorporates southern Thailand, Malaysia, Sumatra, Java, and Borneo (Leakagul and McNeely, 1988; Marwick, 2009). These sub-regions are adaptively significant for plant, insect, amphibian, bird, and mammal taxa (Leakagul and McNeely, 1988; Corbett and Hill, 1992) and were likely also important for hominin dispersals in the past. In recent analyses, parts of Island Southeast Asia, such as Timor, Flores, and Sulawesi, as well as Melanesia, comprise the 'Oceanic' biogeographic zone (Holt et al., 2012) that is bounded to the west by the Wallace Line. Although originally defined on the basis of bird species, this line represents an important adaptive subdivision, with terrestrial mammalian fauna to the east of the line often being limited to smaller marsupial and rodent taxa and considered 'depauperate' (Samper Carro et al., 2016). Interestingly, plants do not follow the division in bird and mammalian taxa to the same extent (Van Welzen et al., 2011).

It is clear that glacial and inter-glacial periods during the Pleistocene would have altered the complexion of these biogeographic divisions (Louys and Turner, 2012). During glacial periods, eustatic reductions in sea level of *c.* 100 m would have exposed 'Sundaland', a landmass that links Mainland Southeast Asia to Sumatra, Java, Borneo, and likely also Melanesia (Bird et al., 2005; Wurster and Bird, 2014). However, it is also apparent that the island of Flores, beyond the Movius line, would have remained separate, necessitating an ocean crossing. Climatic and environmental conditions in the region appear to be tied into these eustatic changes and it has been suggested that a reduction of surface water available for evaporation would have led to the extension of a dry 'savanna corridor' across much of the Sunda shelf during glacial periods (Heaney, 1991; Bird et al., 2005; Rabett, 2012). Such a corridor has been argued to be behind the expansion of large mammals beyond the Wallace line during the Early and Middle Pleistocene (Van den Bergh et al., 2001; Marwick, 2009). Conversely, it provided a barrier to forest-adapted species such as Bornean and Sumatran orangutans, the Sundaland clouded leopard, a suite of murine

rodents, primates, and lowland rainforest bird species (reviewed in Wurster and Bird, 2014). Nevertheless, others have argued that tropical rainforest would have prevailed across Sundaland even during glacial periods (Sun et al., 2000; Hope et al., 2004; Prentice et al., 2011), although regional vegetation models have been largely lacking or constrained by an absence of vegetation-climate feedback and palaeoenvironmental data (Wurster and Bird, 2014).

Debates relating to the presence or absence of tropical rainforest in different parts of Sundaland have remained central to hominin biogeography due to preconceived ideas of the benefits or challenges represented by these habitats. High heat and humidity, disease load, and a lack of large mammalian, or carbohydrate resources have seen them considered impoverished barriers to human foragers (Gamble, 1993; Bird et al., 2005), particularly in insular settings (Samper Carro et al., 2016). Instead maritime adaptations or open grasslands and woodlands have been considered important channels for hominin migration. By contrast, others have highlighted the reliable freshwater and variety of plant and animal taxa afforded by tropical rainforests (Dentan, 1991; Barker et al., 2007; Roberts et al., 2016). It should, however, be noted that the category of 'tropical rainforest' hides considerable complexity, particularly in Southeast Asian and Oceanian contexts and through the course of the Pleistocene (Roberts and Petraglia, 2015; Roberts, 2019). For example, the extent and nature of seasonally cold montane rainforest in Melanesia, the formation of poor-soil peat swamp forest in Mainland and Island Southeast Asia, mangrove coastal forests and their marine resources, and the relative proportions of wet evergreen and drier semi-evergreen rainforest and dry tropical forests in Mainland and Island Southeast Asia will have fluctuated, alongside their unique resources, with changes in temperature, rainfall source and amount, and sea-level (Whitmore, 1998; Louys and Turner, 2012; Wurster and Bird, 2014; Roberts and Petraglia, 2015; Roberts et al., 2016).

Changing climate and sea-level was certainly responsible for dramatic changes in faunal biogeography across the Pleistocene of Southeast Asia and Melanesia (Marwick, 2009). For example, beyond the Wallace line, larger fauna such as *Geochelone* sp. (giant tortoise) and *Stegodon sondaari*, seen in Mainland Southeast Asia, are gradually replaced by smaller mammalian taxa such as *Stegodon floresnsis* and *Hooijeromys nusatenggara* (giant rat) from the Middle Pleistocene (Van den Bergh et al., 1996, 2001), likely due to rising sea-level and increased isolation. Grassland and woodland connections also appear to have facilitated the spread of *Hexaprotodon sivalensis* and *Stegodon trigonocephalus* to Java at the end of the Middle Pleistocene (Van den Bergh et al., 2001). Perhaps the greatest Pleistocene biogeographic shift in Southeast Asia, however, came with the emergence of the so-called Punung fauna, characterized by finds at a site of the same name, that includes *Pongo* (orangutan), *Hylobates* (gibbon) and *Helarctos malayanus* (sun bear) (Van den Bergh et al., 2001). These mammals are also known from Mainland Southeast Asia (Aziz et al., 1995; Long et al., 1996) and represent a southward migration of forest fauna during a period of increased humidity (Van der Kaars and Dam, 1995; Marwick, 2009). This fauna has come to characterize humid forest conditions in the region until today, though it did not extend beyond the Wallace line and into the isolated islands to the East.

4. Swimming with the tide? – Early and Middle Pleistocene *Homo*

As part of the first hominin expansion Out of Africa, by 1.5 Ma there is fossil evidence within the 'Sangiran' geological formation that *H. erectus* had reached beyond the Movius Line and into Java in tropical Southeast Asia (Larick et al., 2001; Zaim et al., 2011) (Fig. 1). The 'Bapang' and 'Trinil' Formations have yielded further fossil evidence for *H. erectus* in excess of 1 Ma in this region (de Vos et al., 1994; Larick et al., 2001). As noted above, however, this Southeast Asian presence is not associated with the distinctive pear-shaped handaxes, commonly associated with *H. erectus*, across Africa (from 1.7 Ma), West Asia, South Asia (1.5 Ma), and Europe (0.9 Ma) (Goren-Inbar et al., 2000; Scott and
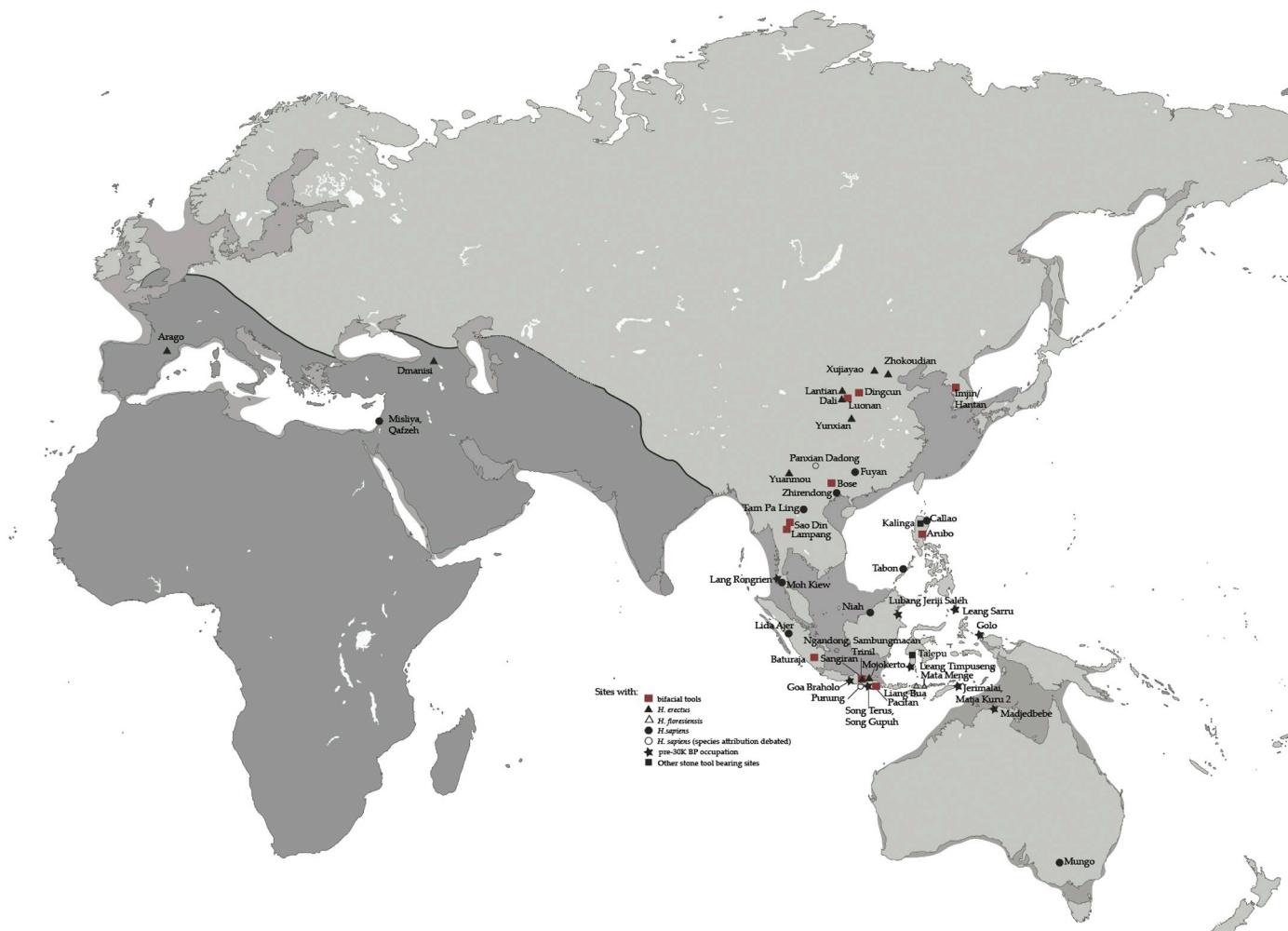
Fig. 1. Map showing the Movius Line and sites in East and Southeast Asia with bifacial tools and hominin remains. See Supplementary Table 1 for the details and references of each site plotted.

Gilbert, 2009), with core and flake toolkits instead being linked with this tropical dispersal. Our knowledge of the routes taken by *pre-H.sapiens* hominins through tropical Southeast Asia remains somewhat obscure. However, there are now three islands with evidence for pre-*H. sapiens* hominins in Wallacea (Dennell et al., 2014; Kaifu, 2017). Firstly, core and flake lithic evidence on Flores now dates to earlier than *c.* 1 Ma (Van den Bergh et al., 1996; Brumm et al., 2010) (Fig. 1). Whether the hominins producing these lithics are closely related to *H. erectus* populations found on Java or represent their own lineage of diminutive hominins (see below) remains debated on the basis of morphology, Pleistocene sea level, and ocean current directions (Dennell et al., 2014; Kaifu, 2017). However, it is clear that these pre-*H. sapiens* members of the genus *Homo* inhabited an island setting with relatively depauperate fauna, through some sort of sea crossing, deliberate or accidental (Smith, 2001), over the longer term.

Elsewhere in Wallacea, lithic artefacts and deliberately modified fauna have now been discovered at the site of Kalinga in the Cagayan valley of the Philippine Archipelago dating to *c.* 709 ka (Ingicco et al., 2018) (Fig. 1). Like Flores, hominin arrival in this part of the world would have necessitated some sort of sea crossing (Ingicco et al., 2018) and, as with Flores, research into ocean currents has been used to argue that the most likely source is Sulawesi, the largest island of Wallacea (Dennell et al., 2014; Ingicco et al., 2018). There is currently no

evidence for *H. erectus* or *H. floresiensis* on this island, though major palaeoanthropological finds that will enrich our knowledge of Pleistocene hominin taxonomy, migration, and biogeography seem certain to emerge in the near future. Indeed, recent evidence from the island indicates the stratigraphic association of stone artefacts with fossil megafauna between 200 and 100 ka that the authors believe are indicative of archaic hominin occupation (Van den Bergh et al., 2016a). Nevertheless, as will be highlighted below, despite this evidence for Early-Middle Pleistocene hominin movement into and within Wallacea there is neither a signature of marine adaptations, or indeed, specialized insular forest adaptations. Indeed, the association of Sulawesi hominin activity with megafaunal *Bubalus* sp., *Stegodon*, and *Celebochoerus* is a trend repeated across Southeast Asia.

In the context of the arrival of *H. erectus* in Java, and Southeast Asia more broadly, between 2.6 and 1 Ma some scholars have argued that tropical rainforest was the dominant vegetation type (Sémah et al., 2002, 2010; Sémah and Sémah, 2012). This supposition is linked to ecological ideas of the stability of evergreen rainforest in this region since the Miocene (Whitmore, 1998). Such a view implies that Early and Middle Pleistocene *Homo* necessarily occupied and exploited tropical forest settings as it moved east of the Movius Line. On the other hand, one of the most prominent hypotheses associated with the first Out of Africa dispersal process has centered on the expansion of open

'savanna' environments (Dennell and Roebroeks, 2005). Dennell and Roebroeks (2005) have argued that the Late Pliocene and Early Pleistocene expansion of a corridor of grasslands ('savannastan'), that occurred in relation to changing atmospheric CO_2 concentrations and orbital characteristics of the Earth, drove the expansion of hominin populations from East Africa into Central Asia. Grasslands in Eurasia at this time are seen as favoring adaptations to long distance ranging and the pursuit of large mammals that are suggested to have characterized the genus *Homo* (Dennell and Roebroeks, 2005). Given the potential effects of changes in sea-level and atmospheric CO_2 driving this process, also likely operated in Southeast Asia during the Quaternary (Heaney, 1991; Gathorne-Hardy et al., 2002), it has also been suggested that 'savanna' or forest-grassland mosaics were crucial for the expansion of *H. erectus* into these regions (Bettis III et al., 2009; Ciochon, 2009).

A lack of well-dated, high-resolution palaeoenvironmental records and detailed archaeological data has made it difficult to distinguish between the hominin use of 'savanna' corridors or tropical forests in Early to Middle Pleistocene Southeast Asia. Although use-wear and residue analyses may, in future, provide insight into the local tropical adaptations exhibited on frequent core and flake industries (e.g. see Xhauflair et al., 2016), information about tool use is currently lacking. As a result, we are currently limited to pollen records and palaeontological records that are both associated and un-associated stratigraphically with Early to Middle Pleistocene hominins. This existing fragmentary evidence highlights an apparent *H. erectus* preference for lake-edge and marsh environments, with sedges and water-tolerant ferns, and perhaps some tropical rainforest fragments (Tonkunaga et al., 1985; Marwick, 2009). Fauna such as pygmy hippo (*Hexaprotodon*), crocodile (*Crocodylus*), tortoise (*Geochelone*), turtles, and fish (de Vos et al., 1994), as well as open woodland-grassland fauna including pigs (*Sus brachygnatus*), cervids (*Axis lydekkeri*), and bovids (*Bubalus palaeokerabau)* (Rozzi et al., 2013), are commonly associated with this hominin in Southeast Asia 1.8–1.0 Ma, emphasizing proximity to rivers or lake-edge environments (Fig. 2). Moreover, the expansion of hominins into Flores *c.* 1–0.8 Ma, the Philippines *c.* 0.7 Ma, and Sulawesi *c.* 0.2–0.1 Ma appears to be linked to the arrival of fauna from the mainland with a preference for grassland and woodland mosaics (Van den Bergh et al., 2001; Van den Bergh et al., 2016a; Ingicco et al., 2018).

Indeed, at every location in modern Mainland or Island Southeast Asia in which *H. erectus* fossils, flake industries, or more rarely bifacial technology, are found in the Early and Middle Pleistocene, the faunal record is dominated by a 'Stegodon' fauna (Marwick, 2009; Van den Bergh et al., 2016a,b) (Fig. 2). Stegodons are extinct proboscideans first documented in a large-bodied form, *S. trigonocephalus*, in the middle Sangiran Formation alongside *H. erectus c.* 1.6–1.5 Ma (Aimi and Aziz, 1985). These animals, closely related to modern elephants, dispersed throughout Island Southeast Asia and, during the Early Pleistocene, appear to have evolved into small-bodied forms in certain isolated islands such as Flores (*S. sondaari*) and Sulawesi (Van den Bergh, 1999). There are several associations of stegodon fossils with early hominin fossils in Island Southeast Asia, implying a potential subsistence association or, at least, similar habitat preferences (Van den Bergh et al., 2001; Brumm et al., 2010). Whatever the exact association, other associated fauna and stable isotope information suggests that these animals, and their hominin co-habitants, inhabited grassland habitats (Brumm et al., 2016), with some potential woodland fragments or riverine settings (Rozzi et al., 2013; Bocherens et al., 2017). It is also clear that climatic and sea-level changes facilitated corridors of movement for these taxa, beyond the Wallace Line onto the island of Flores (Wurster and Bird, 2014), making this a plausible mechanism for hominin expansion.

As noted above, while we have focused on *H. erectus* as the main Early-Middle Pleistocene culprit of hominin expansions in Mainland and Island Southeast Asia it seems increasingly possible that hominins found on Flores may not have been as isolated as it once seemed. Fossil discoveries dated to 0.7 Ma at Mata Menge, Flores (Van den Bergh et al., 2016b), represent a hominin population with small body sizes (Fig. 1), that is seemingly related to later fossils of *H. floresiensis*, the infamous 'Hobbit', now dated to 190–50 ka in Liang Bua Cave, Flores (Moorwood et al., 2004; Sutikna et al., 2016) (Fig. 1), and may also originate from Sulawesi and beyond (Dennell et al., 2014). The exact affinity of this lineage remains debated, with some arguing it represents a Late Pliocene lineage and others arguing it represents a dwarfed *H. erectus* population (Brown et al., 2004; Dennell et al., 2014). Regardless, despite the fact that small body phenotypes in *H. sapiens* are often
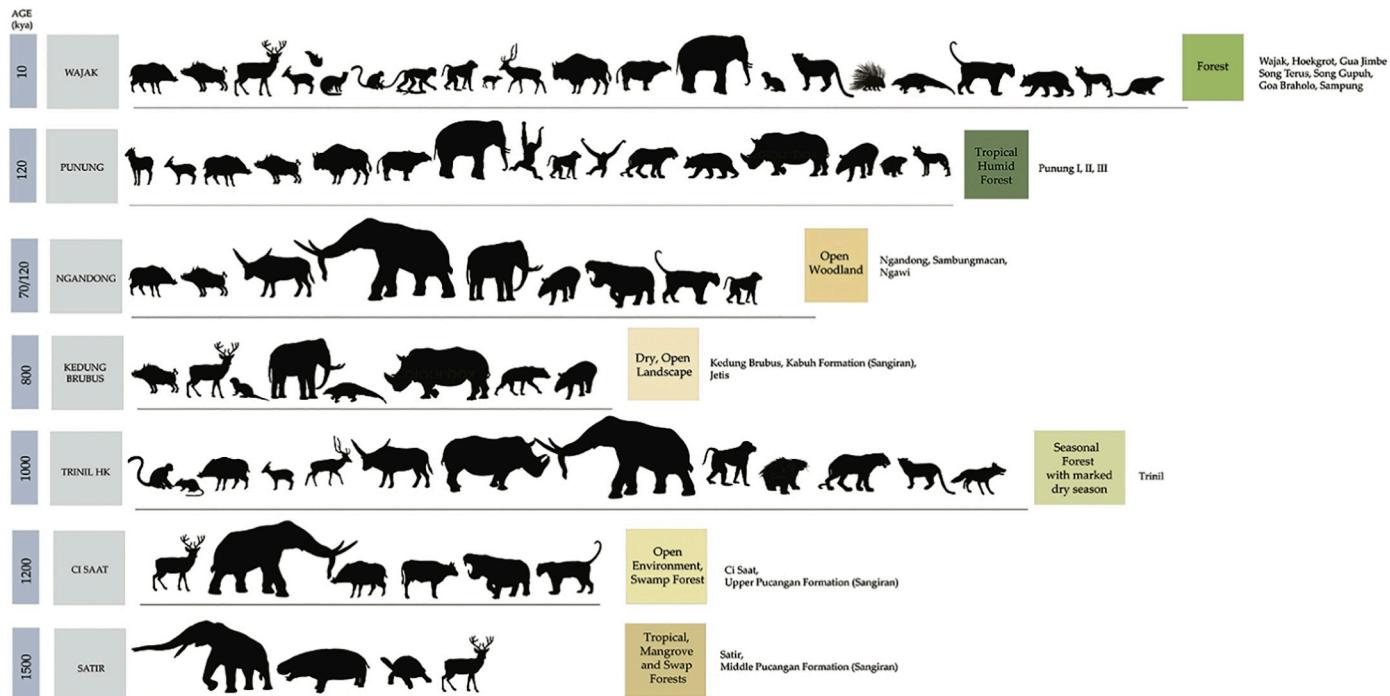

Fig. 2. Faunal turnover scheme for the Pleistocene of Java (after de vos and Sondaar, 1992 and Van den Bergh et al., 2001).
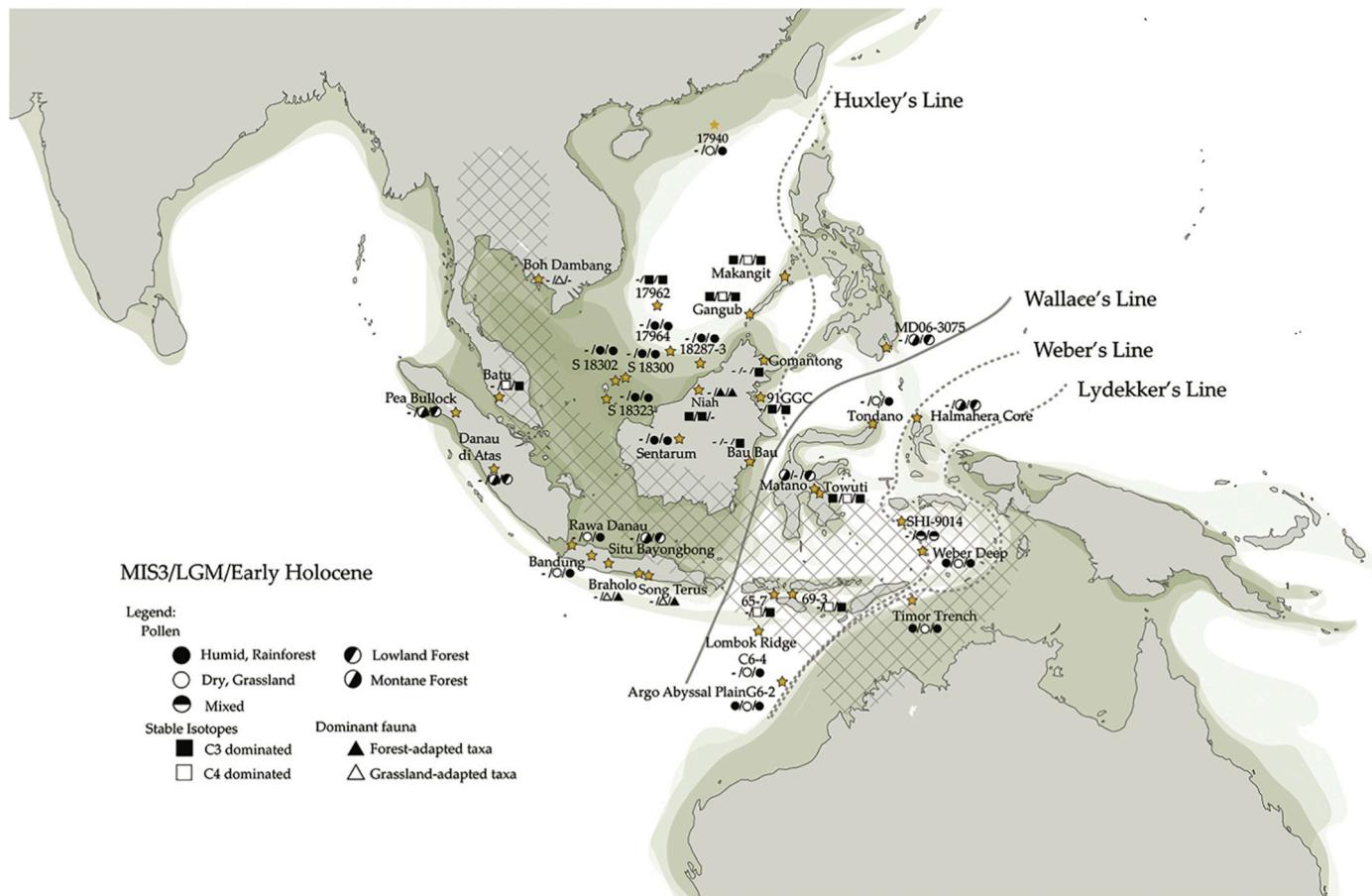
Fig. 3. Summary of the results of paleoenvironmental reconstructions in Island Southeast Asia from MIS3 to the Early Holocene considering different proxies. The map shows the extent of the Sunda shelf during the LGM with the sea level 116 m lower than today (after Voris, 2000; Sathiamurthy and Voris, 2006) and the location of the savanna corridor (grid) proposed by Heaney (1991). (Paleoenvironment data from Van der Kaars, 1991; Barmawidjaja et al., 1993; Van der Kaars and Dam, 1995; Maloney and McCormac, 1996; Newsome and Flenley, 1988; Van der Kaars et al., 2000; Sun et al., 2000, 2002; Dam et al., 2001; Hope, 2001; Hu et al., 2003; Bird et al., 2007; Wurster et al., 2010; Stimpson, 2012; Dubois et al., 2014; Russell et al., 2014.)

linked to adaptive pressures posed by tropical forests, such as isolation and a lack of resources, the palaeoenvironmental evidence shows no such adaptation (Brumm et al., 2016; Van den Bergh et al., 2016a,b). Zooarchaeological, pollen, phytolith, and stable isotope proxy data demonstrates that the Mata Menge fossils are best associated with dry climates and open grassland akin to existing preferences on the Southeast Asian mainland (Brumm et al., 2016). Westaway et al. (2009) argue that *H. floresiensis* occupation intensity at Liang Bua increases during increasingly wet and humid conditions. However, faunal and botanical information, including a reliance on the exploitation of *S. f. insularis* that is associated with stone tools dated to 90–50 ka at the site, implies a preference for woodland and grassland habitats, and competitive scavenging in these settings (Westaway et al., 2009; Meijer and Awe Due, 2010).

Overall then, evaluation of the existing, albeit patchy, evidence for Early and Middle Pleistocene hominin environments in Southeast Asia indicates that *H. erectus* and *H. floresiensis* both appear to be part of a grassland-woodland-dry forest mosaic fauna that expanded across Mainland and Island Southeast Asia during this period. *H. erectus* is, in many places, associated with fragments of lacustrine and riverine tropical forests, and perhaps openings in denser tropical rainforests (de Vos et al., 1994; Rozzi et al., 2013). However, this was always as part of a wider ecological mosaic in which more open, drier woodlands and grasslands dominated. While dense tropical rainforest may have persisted in parts of Southeast Asia through the Early and Middle Pleistocene (Sémah et al., 2002, 2010; Sémah and Sémah, 2012) there is currently no direct evidence that *H. erectus* or *H. floresiensis* either

inhabited or utilized these settings. It is also clear that no Early or Middle Pleistocene hominins made it to Oceania, despite crossing water into Wallacea by 1 Ma, and there is no evidence for these hominins practicing specialized marine or coastal adaptations. On the face of it, therefore, it currently seems that Early and Middle Pleistocene hominins, while perhaps using elements of tropical rainforest, largely followed a fine-tuned adaptive strategy, involving the hunting or scavenging of large grassland-woodland mammals, across the Movius Line and even the Wallace Line.

5. A lesson in flexibility – *Homo sapiens*

It is perhaps telling in this regard that *H. erectus* and *H. floresiensis* apparently become extinct in Southeast Asia alongside a variety of grassland-woodland fauna *c.* 125 ka with the appearance and expansion of modern rainforest fauna (Westaway et al., 2007; Marwick, 2009) (Fig. 2). A premolar possibly dating to earlier than *c.* 100 ka on the island of Java, associated with Punung tropical rainforest fauna, has been argued to represent early human rainforest presence in Indonesia (Storm et al., 2005; Storm and de Vos, 2006; Westaway et al., 2007). Indeed, if the proposed date of *c.* 115–125 ka is correct, this would represent the earliest fossil of our species beyond Africa. However, while the tooth may indeed belong to *H. sapiens*, there remains intense debate relating to the species identification and the date should be treated with skepticism until further work and additional definitive sites of the same age are discovered (Storm et al., 2005; Barker et al., 2007; Bacon et al., 2008; Polanski et al., 2016). Yet, what is clear,

regardless of the position taken on the Punung tooth, is that *H. sapiens* is the only hominin that is found in association with any of this Late Pleistocene fauna in other contexts. This is suggestive of a novel adaptation when compared to the palaeoecological context earlier members of the genus *Homo* in the region reviewed above (Fig. 2). Indeed, Southeast Asia is potentially home to some of the earliest fossils of our species in tropical rainforest contexts globally (Sémah and Sémah, 2015).

Four teeth at Panxian Dadong in South China, dated to 300–130 ka, based on biostratigraphy, U-series, and Electron Spin Resonance dating (Shen et al., 1997; Rink et al., 2003; Schepatz and Miller-Antonio, 2004), have been identified as *H. sapiens* (Schepartz et al., 2000), and associated with fauna indicative of mixed woodland, bamboo forest, and grassland (Schepartz et al. 2000) (Fig. 3). However, the teeth show a clear mix of archaic and derived features, while their chronological association also remains debatable (Liu et al., 2013). Confirmed *H. sapiens* has been found at Fuyan Cave in the same region in association with mixed tropical rainforest, woodland, and grassland fauna (Liu et al., 2015) though the date remains disputed (Michel et al., 2016). Finds of *H. sapiens* associated with rainforest fauna at Lida Ajer in Sumatra *c.* 73–63 ka (Westaway et al., 2017), at Tam Pa Ling, Laos *c.* 60–46 ka associated with some elements of tropical forest microfauna (Demeter et al., 2012, 2015), and a human metatarsal found within a rainforest river valley environment at Callao Cave in the Philippines (Mijares et al., 2010), potentially also represent early human presence in the tropical forests of Southeast Asia (Fig. 2). Famously, the Niah Caves in Sarawak, Borneo have also yielded one of the earliest human fossils, the 'Deep Cave Skull' in an archaeological context in this region (*c.* 44,000–40,000 cal. years BP) (Barker et al., 2007; Higham et al., 2009; Reynolds and Barker, 2015) (Fig. 3).

Indeed, while the dating and environmental context of many of the early fossil finds mentioned above remain disputed, the Niah Caves have yielded some of the most detailed, stratified evidence for Late Pleistocene human rainforest subsistence, dating to between 46,000 and 34,000 cal. years BP, the world over (Barker et al., 2007; Barker, 2013). Sedimentology, pollen analysis, phytolith studies, macrobotanical remains, starch grains, and vertebrate remains have all indicated that human foraging activities were tailored to a tropical forest environment, including the collection and processing of toxic plants and a specialized hunting focus, using some of the earliest bone technology found in Southeast Asia, on wild boar, as well as some arboreal primates (Rabett et al., 2006; Barker et al., 2007; Rabett and Barker, 2007; Barton et al., 2009; Hunt et al., 2012; Piper and Rabett, 2014). Hunt et al. (2012) have also suggested that during periods of maximum forest extent, human groups at the Niah Caves deliberately practiced vegetation burning and disturbance in order to promote the continued presence of a mosaic of evergreen rainforest, peat swamp rainforest, and more open habitats. This fits with evidence from the majority of sites with evidence for early human occupation in Mainland and Island Southeast Asia that indicate a focus on mosaic tropical rainforest habitats (Rabett, 2012; Pawlik et al., 2014; Roberts and Petraglia, 2015) (Fig. 3).

Beyond the Wallace Line, particularly the islands of Timor and Alor that were never connected to Sahul (the continent connecting Melanesia and Australia during glacial declines in sea-level) during the Late Pleistocene, tropical forest use has been considered an unviable source of subsistence for the earliest colonists given depauperate Wallacean insular terrestrial forest environments (O'Connor et al., 2011; Samper Carro et al., 2016). Here, faunal remains, and cultural evidence for pelagic fishing behaviours, from the coastal sites of Jerimalai (45,000–6000 years ago) and Matja Kuru 2 (36,000–10,000 years ago) imply a reliance on marine shellfish, fish, and large marine mammals and turtles (O'Connor et al., 2011; O'Connor, 2015; Samper Carro et al., 2016) (Fig. 3). Shell artefacts, fishhooks, and faunal distributions in the southern Japanese Archipelago dated to *c.* 35,000–13,000 years ago (Fujita et al., 2016), and

similar finds in the Philippines (Pawlik, 2015), further highlight the specialized nature of our species' interaction with marine environments in the Pacific region during this time. Nevertheless, on Timor and Alor, giant rat taxa, with postulated preferences for forest environments, are also present at a number of Late Pleistocene sites (Aplin and Helgen, 2010), while other sites, such as Makpan on Alor, are located inland from the coast (J. Louys pers. comm.), suggesting that our species may also have developed specialized terrestrial adaptations to these island contexts (Fig. 3).

The earliest evidence for the human occupation of Melanesia comes from the Ivane Valley region of Papua New Guinea. Here, at an elevation of *c.* 2000 m, archaeological sites have been radiocarbon dated to between 49,000 and 43,000 cal. years BP at the site of Vilukuav (Summerhayes et al., 2010). Waisted stone axes from the early layers of Airstrip Mound, South Kov, and Kosipe (dated to *c.* 40,000 cal. years BP) have been interpreted as implements used to modify montane rainforest environments (Groube, 1989) (Fig. 3). Starch grains of *Dioscorea* yam species and charred *Pandanus* nuts from radiocarbon-dated Ivane Valley sites also indicate the exploitation of forest products from as early as 49,000–43,000 cal. years BP (Summerhayes et al., 2010). Comparably early evidence for the human occupation of modern-day tropical forests in the Melanesian portion of the Late Pleistocene continent of Sahul has been found elsewhere in Papua New Guinea (Summerhayes et al., 2017) and the Yombon region of West New Britain in the Bismarck Archipelago where the organised utilisation of tropical forest resources is seen *c.* 35,500 cal. years BP (Pavlides and Gosden, 1994; Pavlides, 2004; Summerhayes et al., 2017). Late Pleistocene evidence for human occupation in the tropics of this region has also been documented in New Ireland back to *c.* 40,000 cal. years BP (Leavesley, 2002, 2004, 2005).

In the Ivane Valley of New Guinea, as well as at Late Pleistocene sites in New Ireland such as Buang Merabek, tropical forest foragers have been argued to be small, highly mobile groups, flexibly exploiting local raw materials as part of a seasonal subsistence strategy that made use of a wide variety of environments and negotiated the seasonal extreme cold of the montane rainforests (Pavlides, 2004; Leavesley, 2007; Gosden, 2010; Summerhayes and Ford, 2014; Summerhayes et al., 2017). These populations were also able to exploit the different mammalian resources that existed beyond the Wallace line at this time. As seen at the Niah Caves, these human groups modified their own landscapes. For example, by 20,000 years ago humans moved specie like the bandicoot (*Perameles* sp.) and cuscus (*Phalanger* sp.) between Melanesian islands, including the Bismarck Archipelago, where they are not endemic (Gosden and Robertson, 1991). Supported by patterns in obsidian transport and exploitation, this behaviour suggests humans were moving sources of protein to facilitate colonization and occupation of new settings. The fact that yams (*Discorea alata*) are present on both sides of the Wallace Line by 45 ka has also been linked to intentional human action (Paz, 2005; Summerhayes et al., 2010; Roberts et al., 2017a).

Rabett (2012) has argued that more specialized tropical forest use continued to develop beyond the Movius Line during the Terminal Pleistocene, as precipitation increased and tropical rainforest expanded (though other researchers have suggested rainforest fragmentation – Cannon et al., 2009). It is at this point when complex bone technologies, a diversification of lithic assemblages, and increased selective exploitation of arboreal and semi-arboreal fauna seem to occur across this region simultaneously (Piper and Rabett, 2009; Rabett et al., 2009; Rabett and Piper, 2012). Terrestrial resource use intensifies in Wallacea at this time (O'Connor et al., 2011; Samper Carro et al., 2016), while more dedicated rainforest hunting and gathering strategies have been documented in the Bird's Head Region of Papua New Guinea during the last 26,000 years (Pasveer, 2004). Further sites across the rest of New Ireland (including Buang Merabek, Panakiwuk and Balof) and mainland Papua New Guinea (Nombe, NFX, and Wañelek) also show increasing evidence for human tropical forest presence towards the Terminal

Pleistocene and Early Holocene (Pavlides, 2004; Leavesley, 2007) (Fig. 3). The Early Holocene is also when the earliest firm evidence for human exploitation of tropical evergreen rainforest in Queensland, Australia occurs in the form of the detoxification of toxic forest nuts and the hunting of forest marsupials (Cosgrove et al., 2007; Haberle et al., 2010).

6. Discussion: a real distinction or story of bias?

There is seemingly no cognitive or behavioural reason why Early and Middle Pleistocene members of the genus *Homo* could not have utilized a variety of tropical rainforest, insular, and coastal habitats. Chimpanzees are known to hunt small-bodied tropical forest prey such as colobus monkeys (Stanford et al., 1994), and macaques have been documented exploiting coastal shellfish en-mass (Perry and Codding, 2017). Moreover, *H. erectus* apparently produced abstract designs on freshwater shells at Trinil, Java, Indonesia c. 0.5–0.4 Ma, demonstrating potential symbolic behaviour that was once thought to separate our species cognitively and behaviourally (Joordens et al., 2015). It is therefore possible that the apparent adaptive distinction is linked to taphonomic issues. Early-Middle Pleistocene *Homo* remains and lithic tools are rarely associated with cave or rockshelter sites, or even stratified sites (Roberts et al., 2016). These contexts have been shown to provide well-preserved long-term records of human adaptation from the Late Pleistocene onwards (e.g. Barker et al., 2007; Perera et al., 2011), and the lack of Early-Middle Pleistocene records of this kind, with few exceptions (Sutikna et al., 2016), may mean that long-term sequences associated with Early-Middle Pleistocene activity are biased against, particularly in the tropics. In addition, temporal degradation, particularly if *H. erectus* focused on organic tools in Southeast Asia (Bar-Yosef et al., 2012), may also hamper evidence availability further back in time than the Late Pleistocene.

As a consequence, many early *Homo* sites, even within Africa, are found in lake-edge, swamp, or riverine settings (Barboni et al., 2010; Ashley et al., 2014), meaning that palaeovegetation and palaeontological indicators will inevitably preferentially reflect these habitat types (Roberts et al., 2016). At some locales, such as at Olduvai Gorge, the palaeoenvironmental evidence even implies that Early Pleistocene hominins clustered under woody vegetation (Barboni et al., 2010). Nevertheless, both in Africa, Europe, and Southeast Asia, growing discoveries of Early-Middle Pleistocene *Homo* fossils, stone tool use, symbolic behaviour, and associated palaeoenvironmental information, suggest that the absence of evidence for specialized tropical forest or marine adaptations by our earlier hominin ancestors is not solely a result of preservation bias. The rich multidisciplinary investigations of Liang Bua cave (Sutikna et al. 2016) have also highlighted that detailed palaeoecological and subsistence evidence, site use, and long-term cave sequences can be preserved for late Middle Pleistocene *Homo* in tropical settings (Westaway et al., 2009). Perhaps then, Early-Middle Pleistocene hominin focus on lake and swamp habitats in Southeast Asia and Africa represents a real adaptive emphasis on foraging strategies and home ranges akin to those of large African carnivores rarely found in tropical forests (Turner, 1992; Turner and O'Regan, 2007).

Prey mortality profiles have been used to suggest that Early Pleistocene *Homo* was hunting prime adult bovids at the FLK site of Zinj, Tanzania (Bunn and Gurtov, 2014), perhaps in groups (Bennett et al., 2009), rather than scavenging. The expansion *of H. erectus* beyond Africa and into Eurasia has also been associated with the extinction (perhaps through competition) of large carnivores (Turner, 1992; Turner and O'Regan, 2007). This adaptive model would appear to favour large or middle-sized mammalian game living in open and woodland habitats. *H. floresiensis* also appears to have prioritized the hunting or scavenging of stegodon communities, in competition with other large scavengers, that appear to have favoured similar habitats (Westaway et al., 2009; Meijer and Awe Due, 2010). The general focus of Early to Middle Pleistocene hominins in regions with reliable access

to water, in the form of lakes and rivers, would have provided access to large game populations. Moreover, lakes and rivers would have presented key migration routes for large to medium sized mammals through the tropical region of Southeast Asia (Roberts et al., 2016). Although *H. erectus* was clearly able to make sea crossings into Flores during the Early Pleistocene, this was not accompanied by maritime adaptations and appears to be part of a broader faunal spread and perhaps accidental voyaging (Smith, 2001; Dennell et al., 2014; Van den Bergh et al., 2016b). It therefore seems that for Early-Middle Pleistocene *Homo*, the following of complex grassland-woodland mosaics represented a useful strategy for the crossing of the Movius and Wallace Lines.

By contrast, from at least 45,000 years ago, and perhaps 74,000 years ago or even earlier, our own species crossed the Movius Line using a variety of different environmental adaptations (Kaifu et al., 2015). While in many cases Late Pleistocene sites are associated with complex grassland and forest mosaics, there is also clear evidence for the dedicated use of rainforest plants and animals (Barker et al., 2007; Barker and Farr, 2016) (Fig. 2) and specialized maritime adaptation (O'Connor et al., 2011). Furthermore, our species developed region-specific behaviours in a huge variety of 'tropical rainforest' formations, including mobile lifestyles focused on the use of forest trees and marsupial game in montane New Guinea, the hunting of giant rats on the isolated islands of Timor and Alor, the hunting of arboreal primates and wild boar on Borneo, and pelagic fishing documented in Timor and Alor. In some cases there is also clear evidence for human 'niche' construction and the manipulation of environments, including forest burning (Hunt et al., 2012) and faunal and plant translocation (Gosden and Robertson, 1991; Paz, 2005; Boivin et al., 2016). This engagement with a huge variety of different environments, often with relatively 'simple' core and flake technology (though see Ford, 2017), appears to set apart our species beyond the Movius Line, allowing it to deal with a variety of ecological challenges as the previous hominin inhabitants of Southeast Asia disappeared from the face of the Earth.

Given growing evidence for pre-*H. sapiens* symbolic capacity, sophisticated subsistence strategies, and technological complexity, it is perhaps this plasticity in adaptive specialization that best distinguishes our species. Grove et al. (2015) have similarly argued that our species was uniquely able to adapt to the increasingly frequent climatic fluctuations associated with the Middle-Late Pleistocene and the diverse multitude of Africa's environments that provided the context for the evolution of our species (see also Grove, 2015). Indeed, whether due to cultural or social capacities, our species seems to be unique in its ability to colonize environments (Gamble, 1993; Rabett, 2012). In the context of chimpanzee tropical forest hunting, for example, it is key to note that they do this through tree climbing. Meanwhile, it is now emerging that our species, from as early as 45 ka in Sri Lanka, utilized projectile technology to capture arboreal and semi-arboreal prey from the ground (Wedage et al., in press). While focus on the Movius Line therefore appears to be erroneous in terms of technological or cognitive abilities, it does, perhaps, draw attention to the unique adaptive capacity of our species as a 'plastic pioneer' relative to previous hominins that crossed this notional boundary. Although, the Movius Line is far from being the only geographically relevant area for viewing this phenomenon, given the expansion of our species across the entire face of the planet, it is one case where the colonizing strategies of different hominin species can be compared.

This adaptive distinctiveness of *H. sapiens* beyond the Movius Line could, of course, be easily disproven by the discovery of *H. erectus* or *H. floresiensis* in association with tropical rainforest or maritime resources, or perhaps impoverished fauna in areas beyond the Wallace Line that 'Stegodon' fauna did not reach. Recently, stable carbon and oxygen isotope analysis of Late Pleistocene human tooth enamel has also emerged as a powerful method for testing the reliance of humans on rainforest versus open resources (Roberts et al., 2015, 2017b). Its application to dental enamel of *H. erectus* and *H. floresiensis* from available

sites in Southeast Asia has the potential to determine whether these hominins also relied on rainforest resources dietarily. Isotopic information from associated fauna suggests that *H. erectus* may have inhabited or utilized more densely forested habitats at certain points in time during its existence in Southeast Asia (Janssen et al., 2016), though reliable data from the hominins themselves currently remains lacking. Increasing excavation focus in Southeast Asia, as well as the systematic application of scientific approaches to existing collections, promises the exciting opportunity to test whether our species was indeed unique in its plastic ability to specialize in a variety of newly-colonised environments. Furthermore, additional palaeoanthropological and palaeoenvironmental work across East Asia, including China, promises to contribute to the testing of this proposition significantly in the near future (Bae et al., 2017; Kaifu, 2017), as well as similar discussions about population movements and colonization east to west in this region.

7. Conclusion

It is clear that the Movius Line is no longer relevant as a definitive technological or cognitive boundary for Pleistocene hominins (Lycett and Bae, 2010; Dennell, 2014, 2016). Its geographical focus has also been, in part, dictated by a lack of internationally-available Early-Middle Pleistocene research in eastern and southeastern Asia until recently, and Acheulean and core and flake technologies should not be seen as definitive markers of different cognitive abilities. Instead, technological assemblages should be seen as part of cultural and ecological adaptive strategies to different local contexts and environments. Indeed, the longevity of the Movius Line as a theoretical construct is, in part, a result of palaeoanthropolgocial assumptions of the adaptive challenges involved in crossing this line. To its west, Saharo-Arabian and Afro-tropical biogeographic zones may have represented, at different points in the past, corridors of environmental continuity across much of Africa, Arabia, and western Eurasia in the form of grassland-woodland mosaics (Dennell and Roebroeks, 2005). By contrast, to the east, tropical rainforest and isolated insular settings represent a very different prospect: one that has often been assumed to be an obstacle to hominin occupation and subsistence (Gamble, 1993; Bird et al., 2005; Boivin et al., 2013). Although we do not wish to argue that the Movius Line represents an absolute environmental and adaptive separation, it is potentially useful in considering the varied colonization strategies adopted by Pleistocene hominin species crossing it.

H. erectus, and its diminutive descendant *H. floresiensis*, was able to cross the Movius Line and also the biogeographic division of the Wallace Line. Yet, these species appear to have done so alongside a variety of woodland- and grassland-adapted fauna. While there is tentative evidence for the use of lacustrine and riverine tropical forest settings by these hominins, definitive evidence for adaptations to dense tropical rainforests, or maritime adaptations, during the Early-Middle Pleistocene of Southeast Asia and Melanesia are currently lacking. This suggests that they maintained a relatively homogeneous and specialized adaptation during the colonization of these new regions. By contrast, our species, *H. sapiens*, appeared in Southeast Asia during the expansion of evergreen rainforest fauna that characterizes the humid forests of the region today. Not only that but our species specialized in the colonization of, and adaptation to, a diversity of tropical rainforest settings including high-altitude montane rainforest, depauperate insular forests, peat-swamp forests, as well as wet-dry tropical rainforest mosaics across Southeast Asia and Melanesia. Furthermore, it developed specialized maritime subsistence strategies that aided its expansion beyond the Wallace Line and Sahul. This environmental and adaptive plasticity appears to be unique to our species and may be the reason behind its status as the last hominin on Earth (Roberts and Stewart, 2018).

Declaration of interests

The authors declare no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ara.2019.01.003.

References

Aimi, M., Aziz, F., 1985. Vertebrate fossils from the Sangiran dome, Mojokerto, Trinil, and Sambungmacan areas. In: Watanabe, N., Kadar, D. (Eds.), Quaternary Geology of the Hominid Fossil Bearing Formations in Java. Geological Research and Development Centre, pp. 155–197 Special Publication 4, Bandung, Indonesia.

Ambrose, S.H., 2001. Paleolithic technology and human evolution. Science 291, 1748–1753.

Ambrose, S.H., 2002. Small things remembered: origins of early microlithic industries in Sub-Saharan Africa. In: Elston, R.G., Kuhn, S.L. (Eds.), Thinking Small: Global Perspectives Microlithization. Archaeological Papers of the American Anthropological Association Number 12, Arlington, Virginia, pp. 9–30.

Aplin, K.P., Helgen, K.M., 2010. Quaternary murid rodents of Timor part I: new material of *Coryphomys buehleri* Schaub, 1937, and description of a second species of the genus. Bull. Am. Mus. Nat. Hist. 341, 1–80.

Asfaw, B., Beyene, Y., Suwa, G., Walter, R.C., White, T.D., WoldeGabriel, G., Yemane, T., 1992. The earliest Acheulean from Konso-Gardula. Nature 360, 732–735.

Ashley, G.M., Bunn, H.T., Delaney, J.S., Barboni, D., Dominguez-Rodrigo, M., Mabulla, A.Z.O., Gurtov, A.N., Baluyot, R., Beverly, E.J., Baquedano, E., 2014. Paleoclimatic and paleoenvironmental framework of FLK North archaeological site, Olduvai Gorhe, Tanzania. Quat. Int. 322-323, 54–65.

Aziz, F., de Vos, J., Sondaar, P.Y., van den Bergh, G.D., 1995. *Homo erectus* in SE Asia. Time, space and migration routes: a global model II. In: Proceedings of the International Conference of Human Palaeoontology, Orce.

Bacon, A.-M., Demeter, F., Duringer, P., Helm, C., Bano, M., The Long V, Thi Kim Thuy, N., Antoine, P.-O., Thi Mai, B., Thi Mai Huong, N., Dodo, Y., Chabaux, F., Rihs, S., 2008. The Late Pleistocene Duoi U'Oi cave in northern Vietnam: palaeontology, sedimentology, taphonomy and palaeoenvironments. Quat. Sci. Rev. 27, 1627–1654.

Bae, C.J., Douka, K., Petraglia, M.D., 2017. On the origin of modern humans: Asian perspectives. Science 358, 1–7.

Bailey, R.C., Head, G., Jenike, M., Owen, B., Rechtman, R., Zechenter, E., 1989. Hunting and gathering in tropical rain forest; is it possible? Am. Anthropol. 91, 59–82.

Barboni, D., Ashley, G.M., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.O., Baquedano, E., 2010. Phytoliths infer locally dense and heterogeneous paleovegetation at FLK North and surrounding localities during upper Bed I time, Olduvai Gorge, Tanzania. Quat. Res. 74, 344–354.

Barker, G., 2013. Rainforest Foraging and Farming in Island Southeast Asia, Vol. 1: The Archaeology of the Niah Caves, Sarawak. McDonald Institute Monographs. McDonald Institute for Archaeological Research, Cambridge.

Barker, G., Farr, L. (Eds.), 2016. Archaeological Investigations in the Niah Caves, Sarawak (The Archaeology of the Niah Caves, Sarawak 2). McDonald Institute for Archaeological Research, Cambridge.

Barker, G., Barton, H., Bird, M., Daly, P., Datan, I., Dykes, A., Farr, L., Gilbertson, D., Harrisson, B., Hunt, C., Higham, T., Kealhofer, L., Krigbaum, J., Lewis, H., McLaren, S., Paz, V., Pike, A., Piper, P., Pyatt, B., Rabett, R., Reynolds, T., Rose, J., Rushworth, G., Stephens, M., Stringer, C., Thompson, J., Turney, C., 2007. The 'human revolution' in lowland tropical Southeast Asia: the antiquity and behaviour of anatomically modern humans at Niah Cave (Sarawak, Borneo). J. Hum. Evol. 52, 243–261.

Barmawidjaja, B.M., Rohling, E.J., Van der Kaars, W.A., Grazzini, C.V., Zachariasse, W.J., 1993. Glacial conditions in the northern Molucca Sea region (Indonesia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 101 (1–2), 147–167.

Barton, H., Piper, P.J., Rabett, R., Reeds, I., 2009. Composite hunting technologies from the Terminal Pleistocene and Early Holocene, Niah Cave, Borneo. J. Archaeol. Sci. 36, 1708–1714.

Bar-Yosef, O., Eren, M.I., Yuan, J., Cohen, D.J., Li, Y., 2012. Were bamboo tools made in prehistoric Southeast Asia? An experimental view from South China. Quat. Int. 269, 9–21.

Bellwood, P., 2007. Prehistory of the Indo-Malaysian Archipelago. Australian National University E Press, Canberra, Australia.

Bennett, M.R., Harris, J.W.K., Richmond, B.G., Braun, D.R., Mbua, E., Kiura, P., Olago, D., Kibunjia, M., Omuombo, C., Behrensmeyer, A.K., Huddart, D., Gonzalez, S., 2009. Early hominin foot morphology based on 1.5-million-year-old footprints from Ileret,

Kenya. Science 323, 1197–1201.

Bettis (III), E.A., Milius, A.K., Carpenter, S.J., Larick, R., Zaim, Y., Rizal, Y., Ciochon, R.L., Tassier-Surine, S.A., Murray, D., Suminto Bronto, S., 2009. Way out of Africa: early Pleistocene paleoenvironments inhabited by Homo erectus in Sangiran Java. J. Hum. Evol. 56, 11–24.

Bird, M., Taylor, D., Hunt, C., 2005. Palaeoenvironments of insular Southeast Asia during the last glacial period: a savanna corridor in Sundaland? Quat. Sci. Rev. 24, 2228–2242.

Bird, M.I., Boobyer, E.M., Bryant, C., Lewis, H.A., Paz, V., Stephens, W.E., 2007. A long record of environmental change from bat guano deposits in Makangit Cave, Palawan, Philippines. Earth Environ. Sci. Transact. Roy. Soc. Edinb. 98, 59–69.

Bocherens, H., Schrenk, F., Chaimanee, Y., Kullmer, O., Morike, D., Pushkina, D., Jaeger, J.-J., 2017. Flexibility of diet and habitat in Pleistocene South Asian mammals: implications for the fate of the giant fossil ape *Gigantopithecus*. Quat. Int. 434, 148–155.

Boivin, N., Fuller, D.Q., Dennell, R., Allaby, R., Petraglia, M.D., 2013. Human dispersal across diverse environments of Asia during the Upper Pleistocene. Quat. Int. 300, 32–47.

Boivin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M., Denham, T., Petraglia, M.D., 2016. Ecological consequences of human niche construction: examining long-term anthropogenic shaping of global species distributions. Proc. Natl. Acad. Sci., U. S. A. 113, 6388–6396.

Brown, P., Sutikna, T., Morwood, M.J., Soejono, R.P., Jatmiko Saptomo, E.W., Awe Due, R., 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. Nature 431, 1055–1061.

Brumm, A., 2010. The Movius Line and the Bamboo Hypothesis: early hominin stone technology in Southeast Asia. Lithic Technol. 35, 7–24.

Brumm, A., Moore, M.W., 2012. Biface distributions and the Movius Line: a Southeast Asian perspective. Aust. Archaeol. 74, 32–46.

Brumm, A., Moore, M.W., van den Bergh, G.D., Kurniawan, I., Morwood, M.J., Aziz, F., 2010. Stone technology at the Middle Pleistocene site of Mata Menge, Flores, Indonesia. J. Archaeol. Sci. 37, 451–473.

Brumm, A., van den Bergh, G.D., Storey, M., Kurniawan, I., Alloway, B.V., Setiawan, R., Setyabudi, E., Grün, R., Moore, M.W., Yurnaldi, D., Puspaningrum, M.R., Wibowo, U.P., Insani, H., Sutisna, I., Westgate, J.A., Pearce, N.J.G., Duval, M., Meijer, H.J.M., Aziz, F., Sutikna, T., van der Kaars, S., Flude, S., Morwood, M.J., 2016. Age and context of the oldest known hominin fossils from Flores. Nature 534, 249–253.

Bunn, H.T., Gurtov, N., 2014. Prey mortality profiles indicate that Early Pleistocene Homo at Olduvai was an ambush predator. Quat. Int. 322–323, 44–53.

Cannon, C.H., Morley, R.J., Bush, A.B.G., 2009. The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. Proc. Natl. Acad. Sci. U. S. A. 106, 11188–11193.

Ciochon, R.L., 2009. The mystery ape of Pleistocene Asia. Nature 459, 910–911.

Clark, J.D., 1994. The Acheulian Industrial complex in Africa and elsewhere. In: Curruccini, R.S., Ciochon, R.L. (Eds.), Integrative Paths to the Past: Palaeoanthropological Advances in Honor of F. Clark Howell. New Jersey: Paramount Communications, pp. 451–469.

Corbett, G.B., Hill, J.E., 1992. Mammals of the Indomalayan Region: A Systematic Review. Oxford University Press, Oxford.

Corvinus, G., 2004. Homo erectus in East and Southeast Asia, and the questions of the age of the species and its association with stone artifacts, with special attention to handaxe-like tools. Quat. Int. 117, 141–151.

Cosgrove, R., Field, J., Ferrier, Å., 2007. The archaeology of Australia's tropical rainforests. Palaeogeogr. Palaeoclimatol. Palaeoecol. 251, 150–173.

Dam, R.A., Fluin, J., Suparan, P., van der Kaars, S., 2001. Palaeoenvironmental developments in the Lake Tondano area (N. Sulawesi, Indonesia) since 33,000 yr BP. Palaeogeogr. Palaeoclimatol. Palaeoecol. 171 (3), 147–183.

de Vos, J., Sondaar, P.Y., van den Bergh, G.D., Aziz, F., 1994. The Homo bearing deposits of Java and its ecological context. Courier Forshungsinstitut Senckenberg 171, 129–140.

Demeter, F., Shackelford, L.L., Bacon, A.-M., Duringer, P., Westaway, K., Sayavongkhamdy, T., Braga, J., Sichanthongtip, P., Khamdalavong, P., Ponche, J.-L., Wang, H., Lundstrom, C., Patole-Edoumba, E., Karpoff, A.-M., 2012. Anatomically modern human in Southeast Asia (Laos) by 46 ka. Proc. Natl. Acad. Sci. U. S. A. 109, 14375–14380.

Demeter, F., Schackelford, L., Westaway, K., Duringer, P., Bacon, A.-M., Ponche, J.-L., Wu, X., Sayavongkhamdy, T., Zhao, J.-X., Barnes, L., Boyon, M., Sichanthongtip, P., Sénégas, F., Karpoff, A.-M., Patole-Edoumba, E., Coppens, Y., Braga, J., 2015. Early modern humans and morphological variation in Southeast Asia: fossil evidence from Tam Pa Ling, Laos. PLoS One 10 (4), e0121193.

Dennell, R.W., 2014. Hallam Movius, Helmut de Terra, and the Line that never was: Burma, 1938. In: Boyle, K., Rabett, R.J.C., Hunt, C. (Eds.), Living in the Landscape: Essays in Honour of Graeme Barker. McDonald Institute for Archaeological Research, Cambridge, pp. 11–34.

Dennell, R., 2016. Life without the Movius Line: the structure of the East and Southeast Asian Early Palaeolithic. Quat. Int. 400, 14–22.

Dennell, R.W., Roebroeks, W., 2005. Out of Africa: an Asian perspective on early human dispersal from Africa. Nature 438, 1099–1104.

Dennell, R.W., Louys, J., O'Regan, H.J., Wilkinson, D.M., 2014. The origins and persistence of *Homo floresiensis* on Flores: biogeographical and ecological perspectives. Quat. Sci. Rev. 96, 98–107.

Dentan, R.K., 1991. Potential food sources for foragers in Malaysian rainforest: Sago, yams, and lots of little things. Bijdragen tot de Taal, Land-en Volkenkunde 147, 420–444.

Dubois, N., Oppo, D.W., Galy, V.V., Mohtadi, M., Van Der Kaars, S., Tierney, J.E., Rosenthal, Y., Eglinton, T.I., Lückge, A., Linsley, B.K., 2014. Indonesian vegetation response to changes in rainfall seasonality over the past 25,000 years. Nat. Geosci. 7 (7), 513–517.

Ford, A., 2017. Late Pleistocene lithic technology in the Ivane valley: a view from the rainforest. Quat. Int. 448, 31–43.

Fujita, M., Yamasaki, S., Katagiri, C., Oshiro, I., Sano, K., Kurozumi, T., Sugawara, H.,

Kunikita, D., Matsuzaki, H., Kano, A., Okumura, T., Sone, T., Fujita, H., Kobayashi, S., Naruse, T., Kondo, M., Matsu'ura, S., Suwa, G., Kaifu, Y., 2016. Advanced maritime adaptation in the western Pacific coastal region extends back to 35,000-30,000 years before present. Proc. Natl. Acad. Sci. U. S. A. 113, 11184–11189.

Gamble, C., 1993. Timewalkers: The prehistory of global colonization. Alan Sutton. Stroud.

Gathorne-Hardy, F.J., Syaukani, Davies R.G., Eggleton, P., Jones, D.T., 2002. Quaternary rainforest refugia in south-East Asia: using termites (Isoptera) as indicators. Biol. J. Linn. Soc. 75, 453–466.

Ghazoul, J., Sheil, D., 2010. Tropical Rain Forest Ecology, Diversity, and Conservation. Oxford University Press, Oxford.

Goren-Inbar, N., Feibel, C.S., Verosub, K.L., Melamed, Y., Kislev, M.E., Tchernov, E., Saragusti, I., 2000. Pleistocene Milestones on the Out-of-Africa Corridor at Gesher Benot Ya'aqov, Israel. Science 289, 944–947.

Gorman, C., 1970. Excavations at Spirit Caver, North Thailand: some interim interpretations. Asian Perspect. 13, 79–107.

Gorman, C., 1971. The Hoabinhian and after; Subsistence patterns in Southeast Asia during the Late Pleistocene and early recent periods. World Archaeol. 2, 300–320.

Gosden, C., 2010. When humans arrived in the New Guinea highlands. Science 330, 41–42.

Gosden, C., Robertson, N., 1991. Models for Matenkupkum: interpreting a Late Pleistocene site from Southern New Ireland, Papua New Guinea. In: Allen, J., Gosden, C. (Eds.), Report of the Lapita Homeland Project. Occasional Papers in Prehistory 20. Department of Prehistory. Research School of Pacific Studies, The Australian National University, Canberra, pp. 20–91.

Gowlett, J.A.J., 1984. Mental abilities of early man: a look at some hard evidence. In: Foley, R. (Ed.), Hominid Evolution and Community Ecology. Academic Press, London, UK, pp. 167–192.

Groube, L., 1989. The taming of the rain forests: a model for Late Pleistocene forest exploitation in New Guinea. In: Harris, D.R., Hilman, G.C.H. (Eds.), Foraging and Farming: The Evolution of Plant Exploitation. Unwin, London, pp. 292–304.

Grove, M., 2015. Palaeoclimates, plasticity, and the early dispersal of Homo sapiens. Quat. Int. 369, 17–37.

Grove, M., Lamb, H., Roberts, H., Davies, S., Marshall, M., Bates, R., Huws, D., 2015. Climatic variability, plasiticty, and dispersal: a case study from Lake Tana, Ethiopia. J. Hum. Evol. 87, 32–47.

Haberle, S.G., Rule, S., Roberts, P., Heijnis, H., Jacobsen, G., Turney, C., Cosgrove, R., Ferrier, A., Moss, P., Mooney, S., Kershaw, P., 2010. Paleofire in the wet tropics of Northeast Queensland, Australia. PAGES News 18, 78–80.

Hart, T.B., Hart, J.A., 1986. The ecological basis of hunter-gatherer subsistence in African rain forests. Hum. Ecol. 14, 29–55.

Heaney, L.R., 1991. A synopsis of climatic and vegetational change in Southeast Asia. Clim. Chang. 19, 53–61.

Higham, T.F.G., Barton, H., Turney, C.S.M., Barker, G., Bronk Ramsey, C., Brock, F., 2009. Radiocarbon dating of charcoal from tropical sequences: results from the Niah Great Cave, Sarawak, and their broader implications. J. Quat. Sci. 24, 189–197.

Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jønsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldsa, J., Rahbek, C., 2012. An update of Wallace's zoogeographic regions of the world. Science 339, 74–78.

Hope, G., 2001. Environmental change in the Late Pleistocene and later Holocene at Wanda site, Soroako, South Sulawesi, Indonesia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 171, 129–145.

Hope, G., Kershaw, A.P., van der Kaars, S., Xiangjun, S., Liew, P.-M., Heusser, L.E., Takahara, H., McGlone, M., Miyoshi, N., Moss, P.T., 2004. History of vegetation and habitat change in the Austral-Asian region. Quat. Int. 118-119, 103–126.

Hu, J., Peng, P.A., Fang, D., Jia, G., Jian, Z., Wang, P., 2003. No aridity in Sunda Land during the last glaciation: evidence from molecular-isotopic stratigraphy of long-chain n-alkanes. Palaeogeogr. Palaeoclimatol. Palaeoecol. 201 (3), 269–281.

Hunt, C.O., Gilbertson, D.D., Rushworth, G., 2012. A 50,000-year record of Late Pleistocene tropical vegetation and human impact in lowland Borneo. Quat. Sci. Rev. 37, 61–80.

Ingicco, T., van den Bergh, G.D., Jago-on, C., Bahain, J.-J., Chacón, M.G., Amano, N., Forestier, H., King, C., Manalo, K., Nomade, S., Pereira, A., Reyes, M.C., Sémah, A.-M., Shao, Q., Voinchet, P., Falguères, C., Albers, P.C.H., Lising, M., Yurnaldi, D., Rochette, P., Bautista, A., de Vos, J., 2018. Earliest known hominin activity in the Philippines by 709 thousand years ago. Nature 557, 233–237.

Janssen, R., Joordens, J.C.A., Koutamanis, D.S., Puspaningrum, M.R., de Vos, J., van der Lubbe, J.H.J.L., Reijmer, J.J.G., Hampe, O., Vonhof, H.B., 2016. Tooth enamel stable isotopes of Holocene and Pleistocene fossil fauna reveal glacial and interglacial paleoenvironments of hominins in Indonesia. Quat. Sci. Rev. 144, 145–154.

Ji, X., Kuman, K., Clarke, R.J., Forestier, H., Li, Y., Ma, J., Qiu, K., Li, H., Wu, Y., 2016. The oldest Hoabinhian technocomplex in Asia (43.5 ka) at Xiadong rockshelter, Yunnan Province, Southwest China. Quat. Int. 400, 166–174.

Joordens, J.C.A., d'Errico, F., Wesselingh, F.P., Munro, S., de Vos, J., Walling, J., Ankjærgaard, C., Reimann, T., Wijbrans, J.R., Kuiper, K.F., Mücher, H.J., Coqueugniot, H., Prié, V., Joosten, I., van Os, B., Schulp, A.S., Panuel, M., van der Haas, V., Lustenhouwer, W., Reijmer, J.J.G., Roebroeks, W., 2015. Homo erectus at Trinil on Java used shells for tool production and engraving. Nature 518, 228–231.

Kaifu, Y., 2017. Archaic hominin populations in Asia before the arrival of modern humans: their phylogeny and implications for the "southern Denisovans". Curr. Anthropol. 58, S418–S433.

Kaifu, Y., Izuho, M., Goebel, T., 2015. Modern human dispersal and behavior in palaeolithic Asia: summary and discussion. In: Kaifu, Y., Izuho, M., Goebel, T. (Eds.), Emergence and Diversity of Modern Human Behavior in Paleolithic Asia. Texas, A & M University Press, College Station, pp. 535–566.

Kipfer, B.A., 2000. Hoabinhian. In Encyclopedic Dictionary of Archaeology. Springer Verlag, The Netherlands, pp. 238.

Larick, R., Ciochon, R.L., Zaim, Y., Sudijono, Suminto, Rizal, Y., Aziz, F., Reagan, M., Heizler, M., 2001. Early Pleistocene 40Ar/39Ar ages for Bapang Formation hominins,

Central Jawa, Indonesia. Proc. Natl. Acad. Sci. U. S. A. 98, 4866–4871.

Leakagul, B., McNeely, J.A., 1988. Mammals of Thailand. Association for the Conservation of Wildlife, Bangkok.

Leavesley, M.G., 2002. Buang Merabek: early evidence for human occupation in the Bismarck Archipelago, Papua New Guinea. Aust. Archaeol. 54, 55–57.

Leavesley, M.G., 2004. Trees to the Sky: Prehistoric hunting in New Ireland, Papua New Guinea. PhD thesis. Australian National University, Canberra.

Leavesley, M.G., 2005. Prehistoric hunting strategies in New Ireland, Papua New Guinea: the evidence of the cuscus (*Phalanger orientalis*) remains from Buang Merabak cave. Asian Perspect. 44, 207–218.

Leavesley, M.G., 2007. A shark-tooth ornament from Pleistocene Sahul. Antiquity 81, 308–315.

Li, H., Li, C., Kuman, K., 2014. Rethinking the 'Acheulean' in East Asia: evidence from recent investigations in the Danjiangkou Reservoir Region, Central China. Quat. Int. 347, 163–175.

Li, Y., Zhou, Y., Sun, X., Li, H., 2016. New evidence of a lithic assemblage containing in situ Late Pleistocene bifaces from the Houfang site in the Hanshui River Valley, Central China. Comptes Rendus Palevol. https://doi.org/10.1016/j.crpv.2015.12.005.

Liu, W., Schepartz, L.A., Xing, S., Miller-Antonio, S., Wu, X., Trinkaus, E., Martinón-Torres, M., 2013. Late Middle Pleistocene hominin teeth from Panxian Dadong, South China. J. Hum. Evol. 64, 337–355.

Liu, W., Martinón-Torres, M., Cai, Y.-J., Xing, S., H-w, Tong, S-w, Pei, Sier, M.J., Wu, X.-h., Edwards, R.L., Cheng, H., Y-y, Li, Yang, X.-x., Bermúdez de Casto, J.M., Wu, X.-J., 2015. The earliest unequivocally modern humans in southern China. Nature 526, 696–700.

Long, V.T., de Vos, J., Ciochon, R.S., 1996. The fossil mammal fauna of the Lang Trang caves, Vietnam, compared with Southeast Asian fossil and recent mammal faunas: the geographical implications. Bull. Indo-Pacific Prehistory Assoc. 14, 101–109.

Louys, J., Turner, A., 2012. Environment, preferred habitats and potential refugia for Pleistocene Homo in Southeast Asia. In: Charbonnier, S., Néraudeaux, D. (Eds.), Mainland and Insular Asia: Current Debates About First Settlements. Comptes Rendus Palevol 11pp. 203–211.

Lycett, S.J., Bae, C.J., 2010. The Movius Line controversy: the state of the debate. World Archaeol. 42, 521–544.

Maloney, B.K., McCormac, F.G., 1996. Palaeoenvironments of North Sumatra: a 30,000-year-old pollen record from Pea Bullok. Bull. Indo-Pacific Prehistory Assoc. 14, 73–82.

Marwick, B., 2009. Biogeography of Middle Pleistocene hominins in mainland Southeast Asia: a review of t current evidence. Quat. Int. 202, 51–58.

Matsumura, H., Oxenham, M.F., Lan Cuong, N., 2015. Hoabhinians: A key population with which to debate the peopling of Southeast Asia. In: Kaifu, Y., Izuho, M., Goebel, T. (Eds.), Emergence and Diversity of Modern Human Behavior in Paleolithic Asia. Texas A & M University Press, College Station, pp. 117–132.

Matthews, J.M., 1966. A review of the 'Hoabhinian' in Indo-China. Asian Perspect. 9, 86–95.

Meijer, H.J.M., Awe Due, R., 2010. A new species of giant marabou stork (Aves: Ciconiiformes) from the Pleistocene of Liang Bua, Flores (Indonesia). Zool. J. Linnean Soc. 160, 707–724.

Michel, V., Valladas, H., Shen, G., Wang, W., J-x, Zhao, Shen, C.-C., Valensi, P., Bae, C.J., 2016. The earliest modern Homo sapiens in China? J. Hum. Evol. 101, 101–104.

Mijares, A.S.B., Detroit, F., Piper, P., Grün, R., Bellwood, P., Aubert, M., Champion, G., Cuevas, N., De Leon, A., Dizon, E., 2010. New evidence for a 67,000-year-old human presence at Callao Cave, Luzon, Philippines. J. Hum. Evol. 59, 123–132.

Mishra, S., Gaillard, C., Hertler, C., Moigne, A.-M., Simanjuntak, T., 2010. India and Java: contrasting records, intimate connections. Quat. Int. 223-224, 265–270.

Moorwood, M.J., Soejono, R.P., Roberts, R.G., Sutikna, T., Turney, C.S., Westaway, K.E., Rink, W.J., Zhao, J.X., Van den Bergh, G.D., Due, R.A., Hobbs, D.R., Moore, M.W., Bird, M.I., Fifield, L.K., 2004. Archaeology and age of a new hominin from Flores in eastern Indonesia. Nature 431, 1087–1091.

Movius, H.L., 1944. Early man and Pleistocene stratigraphy in Southern and Eastern Asia. Pap. Peabody Museum Am. Archaeol. Ethnol. I19, 1–125.

Movius, H.L., 1948. The Lower Palaeolithic cultures of Southern and Eastern Asia. Trans. Am. Philos. Soc. 38, 329–420.

Newsome, J., Flenley, J.R., 1988. Late Quaternary vegetational history of the central highlands of Sumatra. II. Palaeopalynology and vegetational history. J. Biogeogr. 1, 555–578.

Norton, C.J., Bae, K., 2008. The Movius Line *sensu lato* (Norton et al. 2006) further assessed and defined. J. Hum. Evol. 55, 1148–1150.

Norton, C.J., Bae, K., Harris, J.W.K., Lee, H., 2006. Middle Pleistocene handaxes from the Korean Peninsula. J. Hum. Evol. 51, 527–536.

O'Connor, S., 2015. Crossing the Wallace line: the maritime skills of the earliest colonists in the Wallacean archipelago. In: Kaifu, Y., Izuho, M., Goebel, T. (Eds.), Emergence and Diversity of Modern Human Behavior in Paleolithic Asia. Texas A & M University Press, College Station, pp. 214–224.

O'Connor, S., Ono, R., Clarkson, C., 2011. Pelagic fishing at 42,000 years before the present and the maritime skills of modern humans. Science 334, 1117–1121.

Pasveer, J.M., 2004. The Djef Hunters: 26,000 Years of Rainforest Exploitation on the Bird's Head of Papua, Indonesia. Balkema, Leiden.

Patole-Edoumba, E., Pawlik, A.F., Mijares, A.S., 2012. Evolution of prehistoric lithic industries of the Philippines during the Pleistocene. Comp. Rend. Palevol. 11, 213–230.

Pavlides, C., 2004. From Misisil Cave to Eliva hamlet: rediscovering the Pleistocene in interior West New Britain. In: Auenbrow, V., Fullager, R. (Eds.), A Pacific Odyssey: Archaeology and Anthropology in the Western Pacific. Papers in Honour of Jim Specht. Records of the Australian Museum, Supplement 29 Sydney, Australian Museum, pp. 97–108.

Pavlides, C., Gosden, C., 1994. 35,000-year-old sites in the rainforests of West New Britain, Papua New Guinea. Antiquity 68, 604–610.

Pawlik, A., 2004. The Paleolithic Site of Arubo 1 in Cental Luzon, Philippines. IPPA Bull. 2, 3–12.

Pawlik, A., 2015. Detecting traits of modern behavior through microwear analysis: a case study from the Philippine terminal Pleistocene. In: Kaifu, Y., Izuho, M., Goebel, T. (Eds.), Emergence and Diversity of Modern Human Behavior in Paleolithic Asia. Texas A & M University Press, College Station, pp. 182–199.

Pawlik, A.F., Piper, P.J., Mijares, A.S.B., 2014. Modern humans in the Philippines: colonization, subsistence and new insights into behavioural complexity. In: Dennell, R., Poor, M. (Eds.), Southern Asia, Australia and the Search for Human Origins. Cambridge University Press, Cambridge, pp. 135–147.

Paz, V.J., 2005. Rock shelters, caves, and archaeobotany in island Southeast Asia. Asian Perspect. 44, 107–118.

Perera, N., Kourampas, N., Simpson, I.A., Deraniyagala, S.U., Bulbeck, D., Kamminga, J., Perera, J., Fuller, D.Q., Szabo, K., Oliveira, N.V., 2011. People of the ancient rainforest: Late Pleistocene foragers at the Batadomba-lena rockshelter, Sri Lanka. J. Hum. Evol. 61, 254–269.

Perry, G.H., Codding, B.F., 2017. Monkeys overharvest shellfish. elife 6, e30865.

Petraglia, M.D., Shipton, C., 2008. Large cutting tool variation west and east of the Movius Line. J. Hum. Evol. 55, 962–966.

Piper, P.J., Rabett, R.J., 2009. Disentangling the Harrisson archive to interpret the spatial and temporal distribution of vertebrate remains at Niah Caves, Borneo. Int. J. Osteoarchaeol. 19, 464–475.

Piper, P.J., Rabett, R.J., 2014. Late Pleistocene subsistence strategies in Island Southeast Asia and their implications for understanding the development of modern human behaviour. In: Dennell, R., Poor, M. (Eds.), Southern Asia, Australia and the Search for Human Origins. Cambridge University Press, Cambridge, pp. 118–134.

Polanski, J.M., Marsh, H.E., Maddux, S.D., 2016. Dental size reduction in Indonesian *Homo erectus*: implications for the PU-198 premolar and the appearance of *Homo sapiens* on Java. J. Hum. Evol. 90, 49–54.

Prentice, I.C., Harrison, S.P., Bartlein, P.J., 2011. Global vegetation and terrestrial carbon cycle changes after the last ice age. New Phytol. 189, 988–998.

Rabett, R.J., 2012. Human Adaptation in the Asian Palaeolithic. Cambridge University Press, Cambridge.

Rabett, R.J., Barker, G., 2007. Through the looking glass: new evidence on the presence and behaviour of Late Pleistocene humans at Niah Cave, Sarawak, Borneo. In: Mellars, P., Boyle, K., Bar-Yosef, O., Stringer, C. (Eds.), Rethinking the Human Revolution. McDonald Institute for Archaeological Research, Cambridge, pp. 383–394.

Rabett, R.J., Piper, P.J., 2012. The emergence of bone technologies at the end of the Pleistocene in Southeast Asia: regional and evolutionary implications. Camb. Archaeol. J. 22, 37–56.

Rabett, R.J., Piper, P.J., Barker, G., 2006. Bones from Hell: preliminary results of new work on the Harrisson faunal assemblage from the deepest part of Niah Cave, Sarawak. In: Bacus, E.A., Glover, I.C., Pigott, V.C. (Eds.), Uncovering Southeast Asia's Past: Selected Papers from the 10th International Conference of the European Association of Southeast Asian Archaeologists. NUS Press, Singapore, pp. 46–59.

Rabett, R., Barker, G., Hunt, C., Naruse, T., Piper, P., Raddatz, E., Reynolds, T., Nguyen, V.S., Stimpson, C., Szabo, K., Nguyen, C.T., Wilson, J., 2009. The Trang an project: Late-to-post-pleistocene settlement of the lower song Hong Valley, North Vietnam. J. Roy. Asiatic Soc. Great Brit. Ireland 19, 83–109.

Reynolds, T., Barker, G., 2015. Reconstructing Late Pleistocene climates, landscapes, and human activities in northern Borneo from excavations in the Niah Caves. In: Kaifu, Y., Izuho, M., Goebel, T. (Eds.), Emergence and Diversity of Modern Human Behavior in Paleolithic Asia. Texas A & M University Press, College Station, pp. 140–157.

Rink, W.J., Schepartz, L.A., Miller-Antonio, S., Huang, W.W., Hou, Y., Bakken, D., Richter, D., Jones, H.L., 2003. Electron spin resonance (ESR) dating of mammalian tooth enamel Panxian Dadong Cave, Guizhou, China. In: Shen, C., Keates, S. (Eds.), Current Research in Chinese Pleistocene Archaeology. Oxford: BAR International Series 117pp. 111–118..

Roberts, P., 2019. Tropical Forests in Prehistory, History, and Modernity. Oxford University Press, Oxford.

Roberts, P., Petraglia, M.D., 2015. Pleistocene rainforests: barriers or attractive environments for early human foragers? World Archaeol. 47, 718–739.

Roberts, P., Stewart, B., 2018. Defining the 'generalist-specialist' niche for Pleistocene *Homo sapiens*. Nat. Hum. Behav. https://doi.org/10.1038/s41562-018-0394-4.

Roberts, P., Perera, N., Wedage, O., Deraniyagala, S.U., Perera, J., Eregama, S., Gledhill, A., Petraglia, M., Lee-Thorp, J., 2015. Direct evidence for human rainforest resource reliance in Late Pleistocene Sri Lanka. Science 347, 1246–1249.

Roberts, P., Boivin, N., Lee-Thorp, J., Petraglia, M., Stock, J., 2016. Tropical forests and the genus *Homo*. Evol. Anthropol. 25, 306–317.

Roberts, P., Hunt, C., Arroyo-Kalin, M., Evans, D., Boivin, N., 2017a. The deep human prehistory of global tropical forests and its relevance for modern conservation. Nat. Plants 3, 17093.

Roberts, P., Perera, N., Wedage, O., Deraniyagala, S., Perera, J., Eregama, S., Gledhill, A., Petraglia, M.D., JA, JLee-Thorp, 2017b. Fruits of the forest: human stable isotope ecology and rainforest adaptations in Late Pleistocene and Holocene (~ 36 to 3 ka) Sri Lanka. J. Hum. Evol. 106, 102–118.

Rozzi, R., Winkler, D.E., De Vos, J., Schulz, E., Palombo, M.R., 2013. The enigmatic bovid Duboisia santeng (Dubois, 1891) from the Early-Middle Pleistocene of Java: a multiproxy approach to its paleoecology. Palaeogeogr. Palaeoclimatol. Palaeoecol. 377, 73–85.

Russell, J.M., Vogel, H., Konecky, B.L., Bijaksana, S., Huang, Y., Melles, M., King, J.W., 2014. Glacial forcing of central Indonesian hydroclimate since 60,000 y BP. Proc. Natl. Acad. Sci. 111 (14), 5100–5105.

Samper Carro, S.C., O'Connor, S., Louys, J., Hawkins, S., Mahirta, M., 2016. Human maritime subsistence strategies in the Lesser Sunda Islands during the terminal Pleistocene-early Holocene: new evidence from Alor, Indonesia. Quat. Int. 416, 64–79.

Sathiamurthy, E., Voris, H.K., 2006. Maps of Holocene sea level transgression and submerged lakes on the Sunda shelf. Nat. Hist. J. Chulalongkorn Univ. Suppl. 2, 1–43.

Schepatz, L., Miller-Antonio, S., 2004. Asia and the Middle Pleistocene in global perspective. Asian Perspect. 43, 187–366.

Schepartz, L.A., Miller-Antonio, S., Bakken, D.A., 2000. Upland resources and the early Palaeolithic occupation of southern China, Vietnam, Laos, Thailand and Burma. World Archaeology 32 (1), 1–13.

Schick, K.D., 1994. The Movius Line reconsidered: perspectives on Early Paleolithic of Eastern Asia. In: Corruccini, R.S., Ciochon, R.L., Howell, F.C. (Eds.), Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell. Prentice Hall, London, pp. 569–596.

Schick, K.D., Zhuan, D., 1993. Early Paleolithic of China and Eastern Asia. Evol. Anthropol. 2, 22–35.

Scott, G.R., Gilbert, L., 2009. The oldest Handaxes in Europe. Nature 461, 82–85.

Sémah, A.-M., Sémah, F., 2012. The rain forest in Java through the Quaternary and its relationships with humans (adaptation, exploitation and impact on the forest). Quat. Int. 249, 120–128.

Sémah, A.-M., Sémah, F., 2015. Tracking evidence for modern human behavior in Paleolithic Indonesia. In: Kaifu, Y., Izuho, M., Goebel, T. (Eds.), Emergence and Diversity of Modern Human Behavior in Paleolithic Asia. Texas A & M University Press, College Station, pp. 158–170.

Sémah, F., Sémah, A.-M., Simanjuntak, T., 2002. More than a million years of human occupation in insular Southeast Asia: the early archaeology of eastern and Central Java. In: Mercader, J. (Ed.), Under the Canopy: The Archaeology of Tropical Rain Forests. Rutgers University Press, Piscataway, New Jersey, pp. 161–190.

Sémah, A.M., Sémah, F., Djubiantono, T., Brasseur, B., 2010. Landscapes and Hominids' environments: changes between the Lower and the Early Middle Pleistocene in Java (Indonesia). Quat. Int. 223-224, 451–454.

Shen, G., Liu, J., Jin, L., 1997. Preliminary results on U-series dating of Panxian Dadong in Guizhou Province, S-W China. Acta Anthropol. Sin. 16, 221–230.

Smith, J.M.B., 2001. Did early hominids cross sea gaps on natural rafts? In: Metcalf, I., Smith, J., Davidson, I., Morwood, M.J. (Eds.), Faunal and Floral Migrations and Evolution in SE Asia-Australasia. Swets and Zetilinger, The Netherlands, pp. 409–416.

Stanford, C.B., Wallis, J., Matama, H., Goodall, J., 1994. Patterns of predation by chimpanzees on red colobus monkeys in Gombe national park, 1982–1991. Am. J. Phys. Anthropol. 94, 213–228.

Stimpson, C.M., 2012. Local scale, proxy evidence for the presence of closed canopy forest in North-western Borneo in the Late Pleistocene: bones of strategy I bats from the archaeological record of the Great Cave of Niah, Sarawak. Palaeogeogr. Palaeoclimatol. Palaeoecol. 331, 136–149.

Storm, P., de Vos, J., 2006. Rediscovery of the Late Pleistocene Punung hominin sites and the discovery of a new site Gunung Dawung in East Java. Senckenb. Lethaea 86, 271–281.

Storm, P., Aziz, F., de Vos, J., Kosasih, D., Baskoro, S., Ngaliman va den Hoek Ostende, L.W., 2005. Late Pleistocene *Homo sapiens* in a tropical rainforest fauna in East Java. J. Hum. Evol. 49, 536–545.

Sutikna, T., Tocheri, M.W., Morwood, M.J., Saptomo, E.W., Awe, R.D., Wasisto, S., Westaway, K.E., Aubert, M., Li, B., Zhao, J.X., Storey, M., Alloway, B.V., Morley, M.W., Meijer, H.J.M., van den Bergh, G., Grun, R., D'Osseto, A., Brumm, A., Jungers, W.L., Roberts, R.G., 2016. Revised stratigraphy and chronology for Homo floresiensis at Liang Bua in Indonesia. Nature 532 (7599), 366–369.

Summerhayes, G.R., Ford, A., 2014. Late Pleistocene colonisation and adaptation in New Guinea: implications for modeling modern human behaviour. In: Dennell, R., Poor, M. (Eds.), Southern Asia, Australia and the Search for Human Origins. Cambridge University Press, Cambridge, pp. 213–227.

Summerhayes, G.R., Leavesley, M., Fairbairn, A., Mandui, H., Field, J., Ford, A., Fullagar, R., 2010. Human adaptation and plant use in Highland New Guinea 49,000 to 44,000 years ago. Science 330, 78–81.

Summerhayes, G.R., Field, J.H., Shaw, B., Gaffney, D., 2017. The archaeology of forest exploitation and change in the tropics during the Pleistocene: the case of Northern Sahul (Pleistocene New Guinea). Quat. Int. 448, 14–30.

Sun, X., Li, X., Luo, Y., Chen, X., 2000. The vegetation and climate at the last glaciation on the emerged continental shelf of the South China Sea. Palaeogeogr. Palaeoclimatol. Palaeoecol. 160, 301–316.

Sun, X., Li, X., Luo, Y.L., 2002. Vegetation and climate on the Sunda Shelf of the South China Sea during the last glaciation—pollen results from Station 17962. Acta Bot. Sin. 44 (6), 746–752.

Sutikna, T., Tocheri, M.W., Morwood, M.J., Saptomo, E.W., Jatmiko, Due Awe, R., Wasisto, S., Westaway, K.E., Aubert, M., Li, B., Zhao, J.-x., Storey, M., Alloway, B.V., Morley, M.W., HJM, Meijer, van den Bergh, G.D., Grün, R., Dosseto, A., Brumm, A., Jungers, W.L., Roberts, R.G., 2016. Revised stratigraphy and chronology for *Homo floresiensis* at Liang Bua in Indonesia. Nature 532, 366–369.

Tonkunaga, S., Oshima, H., Polhaupesy, A., Ito, Y., 1985. A palynological study of the Pucan- gan and Kabuh formations in the Sangiran area. In: Watanabe, N., Kadar, D. (Eds.), Quaternary Geology of the Hominid Fossil Bearing Formations in Java. Bandung, Geological Research and Development Centre, pp. 199–217.

Turner, A., 1992. Large carnivores and earliest European hominids: changing determinants of resource availability during the Lower and Middle Pleistocene. J. Hum. Evol. 22, 109–126.

Turner, A., O'Regan, H.J., 2007. Afro-Eurasian mammalian fauna and early hominin dispersals. In: Petraglia, M.D., Allchin, B. (Eds.), The Evolution and History of Human Populations in South Asia. Springer, Dordrecht, pp. 23–39.

Van den Bergh, G.D., 1999. The late Negone elephantoid-bearing faunas of Indonesia and their palaeozoogeographic. A study of the terrestrial faunal succession of Sulawesi, Flores and Java, including evidence for early hominid dispersal east of Wallace's Line implications. Scr. Geol. 117, 1–419.

Van den Bergh, G.D., de Vos, J., Sondaar, P.Y., Aziz, F., 1996. Pleistocene zoogeographic evolution of Java (Indonesia) and glacio-eustatic sea level fluctuations: a background for the presence of *Homo*. Bull. Indo-Pacific Prehistory Assoc. 14, 7–21.

Van den Bergh, G.D., de Vos, J., Sondaar, P.Y., 2001. The Late Quaternary palaeogeography of mammal evolution in the Indonesian Archipelago. Palaeogeogr. Palaeoclimatol. Palaeoecol. 171, 385–408.

Van den Bergh, G.D., Bo, L., Brumm, A., Grün, R., Yurnaldi, D., Moore, M.W., Kurniawan, I., Setiawan, R., Aziz, F., Roberts, R.G., Suyono, Storey M., Setiabudi, E., Morwood, M.J., 2016a. Earliest hominin occupation of Sulawesi, Indonesia. Nature 529, 208–211.

Van den Bergh, G.D., Kaifu, Y., Kurniawan, I., Kono, R.T., Brumm, A., Setiyabudi, E., Aziz, F., Morwood, M.J., 2016b. *Homo floresiensis*-like fossils from the early Middle Pleistocene of Flores. Nature 534, 245–248.

Van der Kaars, W.A., 1991. Palynology of eastern Indonesian marine piston-cores: a Late Quaternary vegetational and climatic record for Australasia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 85 (3–4), 23926–23931.

Van der Kaars, W.A., Dam, M.C., 1995. A 135,000-year record of vegetational and climatic change from the Bandung area, West-Java, Indonesia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 117, 55–72.

Van der Kaars, W.A., Wang, X., Kershaw, P., Guichard, F., Setiabudi, D.A., 2000. A Late Quaternary palaeoecological record from the Banda Sea, Indonesia: patterns of vegetation, climate and biomass burning in Indonesia and northern Australia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 155, 135–153.

Van Welzen, P.C., Parnell, J.AN., Slik, J.W.F., 2011. Wallace's Line and plant distributions: two or three phytogeographical areas and where to group Java? Biol. J. Linn. Soc. 103, 531–545.

Voris, H.K., 2000. Maps of Pleistocene Sea levels in Southeast Asia: shore- lines, river systems and time durations. J. Biogeogr. 27, 1123–1157.

Wang, W., Lycett, S.J., von Cramon-Taubadel, N., Jin, J.J.H., Bae, C.J., 2012. Comparison of handaxes from Bose Basin (China) and the western Acheulean indicates convergence of form, not cognitive differences. PLoS ONE 7, e35804.

Watts, D., 1984. The spatial dimension in biogeography. In: Taylor, J. (Ed.), Themes in Biogeography. Croom Helm, London.

Wedage, O., Amano, N., Langley, M.C., Douka, K., Blinkhorn, J., Crowther, A., Deraniyagala, S., Kourampas, N., Simpson, I., Perera, N., Picin, A., Boivin, N., Petraglia, M., Roberts, P., 2019. Specialized rainforest hunting by Homo sapiens ~ 45,000 years ago. Nature Communications (in press).

West, J., Louys, J., 2007. Differentiating bamboo from stone tool cut marks in the zooarchaeological record, with a discussion on the use of bamboo knives. J. Archaeol. Sci. 34, 512–518.

Westaway, K.E., Morwood, M.J., Roberts, R.G., Rokus, A.D., Zhao, J.X., Storm, P., Aziz, F., Van Den Bergh, G., Hadi, P., Jatmiko, De Vos, J., 2007. Age and biostratigraphic significance of the Punung Rainforest Fauna, East Java, Indonesia, and implications for Pongo and Homo. J. Hum. Evol. 53, 709–717.

Westaway, K.E., Morwood, M.J., Sutikna, T., Moore, M.W., Rokus, A.D., van den Bergh, G.D., Roberts, R.G., Saptomo, E.W., 2009. *Homo floresiensis* and the Late Pleistocene environments of Eastern Indonesia: defining the nature of the relationship. Quat. Sci. Rev. 28, 2897–2912.

Westaway, K.E., Louys, J., Due Awe, R., Morwood, M.J., Price, G.J., Zhao, J.-X., Aubert, M., Joannes-Boyau, R., Smith, T.M., Skinner, M.M., Compton, T., Bailey, R.M., Van den Bergh, G.D., de Vos, J., Pike, A.W.G., Stringer, C., Saptomo, E.W., Rizal, Y., Zaim, J., Santoso, W.D., Trihascaryo, A., Kinsley, L., Sulistyanto, B., 2017. An early modern human presence in Sumatra 73,000-63,000 years ago. Nature 548, 322–325.

Whitmore, T.C., 1998. An Introduction to Tropical Rainforests, 2nd ed. Oxford University Press, Oxford.

Wurster, C.M., Bird, M.I., 2014. Barriers and bridges: early human dispersals in equatorial SE Asia. In: Harff, J., Bailey, G., Lüth, F. (Eds.), Geology and Archaeology: Submerged Landscapes of the Continental Shelf. Geological Society, London (Special Publications, 411).

Wurster, C.M., Bird, M.I., Bull, I.D., Creed, F., Bryant, C., Dungait, J.A.J., Paz, V., 2010. Forest contraction in north equatorial Southeast Asia during the Last Glacial Period. Proc. Natl. Acad. Sci. 107 (35), 15508–15511.

Wynn, T., 1991. Tools, grammar, and the archaeology of cognition. Camb. Archaeol. J. 1, 191–206.

Xhauflair, H., Pawlik, A., Gaillard, C., Forestier, H., Vitales, T.J., Callado, J.R., Tandang, D., Amano, N., Manipon, D., Dizon, E., 2016. Characterisation of the user-wear resulting from bamboo working and its importance to address the hypothesis of the existence of a bamboo industry in prehistoric Southeast Asia. Quat. Int. 416, 95–125.

Zaim, Y., Ciochon, R.L., Polanski, J.M., Grine, F.E., Bettis III, E.A., Rizal, Y., Franciscus, R.G., Larick, R.R., Heizler, M., Aswan Eaves, K.L., Marsh, H.E., 2011. New 1.5 million-year-old Homo erectus maxilla from Sangiran (Central Java, Indonesia). J. Hum. Evol. 61, 363–376.